An Amazonian rainforest and its fragments as a laboratory of global change

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ABSTRACT

We synthesize findings from one of the world's largest and longest-running experimental investigations, the Biological Dynamics of Forest Fragments Project (BDFFP). Spanning an area of ~1,000 km^2 in central Amazonia, the BDFFP was initially designed to evaluate the effects of fragment area on rainforest biodiversity and ecological processes. However, over its 38-year history to date the project has far transcended its original mission, and now focuses more broadly on landscape dynamics, forest regeneration, regional- and global-change phenomena, and their potential interactions and implications for Amazonian forest conservation. The project has yielded a wealth of insights into the ecological and environmental changes in fragmented forests. For instance, many rainforest species are naturally rare and hence are either missing entirely from many fragments or so sparsely represented as to have little chance of long-term survival. Additionally, edge effects are a prominent driver of fragment dynamics, strongly affecting forest microclimate, tree mortality, carbon storage and a diversity of fauna.

Even within our controlled study area, the landscape has been highly dynamic: for example, the matrix of vegetation surrounding fragments has changed markedly over time, succeeding from large cattle pastures or forest clearcuts to secondary regrowth forest. This, in

turn, has influenced the dynamics of plant and animal communities and their trajectories of change over time. In general, fauna and flora have responded differently to fragmentation: the most locally extinction-prone animal species are those that have both large area requirements and low tolerance of the modified habitats surrounding fragments, whereas the most vulnerable plants are those that respond poorly to edge effects or chronic forest disturbances, and that rely on vulnerable animals for seed dispersal or pollination.

Relative to intact forests, most fragments are hyperdynamic, with unstable or fluctuating populations of species in response to a variety of external vicissitudes. Rare weather events such as droughts, windstorms and floods have had strong impacts on fragments and left lasting legacies of change. Both forest fragments and the intact forests in our study area appear to be influenced by larger-scale environmental drivers operating at regional or global scales. These drivers are apparently increasing forest productivity and have led to concerted, widespread increases in forest dynamics and plant growth, shifts in tree-community composition, and increases in liana (woody vine) abundance. Such large-scale drivers are likely to interact synergistically with habitat fragmentation, exacerbating its effects for some species and ecological phenomena. Hence, the impacts of fragmentation on Amazonian biodiversity and ecosystem processes appear to be a consequence not only of local site features but also of broader changes occurring at landscape, regional and even global scales.

Key words: Amazonia, biodiversity, carbon storage, climate change, drought, ecosystem services, edge effects, environmental synergisms, habitat fragmentation, nature reserves.

CONTENTS

I. INTRODUCTION

The Biological Dynamics of Forest Fragments Project (BDFFP) is the world's largest and longest-running experimental study of habitat fragmentation (Lovejoy *et al.*, 1986; Bierregaard *et al.*, 1992; Laurance *et al.*, 2002, 2011). Located in central Amazonia (Fig. 1), the BDFFP has evolved since its inception in 1979 into an epicenter for long-term research. Beyond this, its research mission has gradually broadened to include not only forest fragmentation but also studies of forest regeneration, landscape dynamics, climatic variation, regional- and global-change phenomena and a variety of interdisciplinary research topics.

The BDFFP is strategically located at the heart of the Amazon, the world's largest tropical forest. The Amazon itself lies at the intersection of key questions in global change, both for research and for action. It is believed to be one of the major regions that will be most impacted by projected climatic change (Salazar *et al.*, 2007; Dai, 2012; IPCC, 2013; Nobre *et al.*, 2016). If effectively conserved and managed, the Amazon has the potential to contribute markedly to efforts to limit climate change during the narrow window of time we have remaining to avert 'dangerous' global warming (Fearnside, 2000, 2012; Houghton *et al.*, 2015). Because of its enormous carbon-storage capacity, it is also one of the places on Earth where sharply reducing greenhouse-gas emissions could be achieved by limiting forest loss and degradation, thereby delivering great global benefits for humankind (Stickler *et al.*, 2009).

Today, the BDFFP is one of the most enduring, influential and highly cited environmental investigations in the world (Gardner *et al.*, 2009; Peres *et al.*, 2010; Pitman *et al.*, 2011). Its wide-ranging research has involved hundreds of Brazilian and international investigators and thousands of students and other trainees. Here we synthesize the contributions of this singular project to the study of habitat fragmentation, including its broader consequences for Amazonian ecosystems and biota. We emphasize that many of the

local impacts of fragmentation in the Amazon are being modified or exacerbated by environmental changes occurring at wider landscape, regional and even global scales. We assert that the effects of fragmentation cannot be fully understood without considering the influence of these larger-scale phenomena.

II. LARGER-SCALE DRIVERS

(1) Landscape-scale phenomena

The correlated processes of forest loss and fragmentation are among the greatest threats to tropical biodiversity (Lovejoy *et al.*, 1986; Ewers & Didham, 2006; Laurance & Peres, 2006; Gibson *et al.*, 2011). Amazonia harbors more than half of the world's surviving tropical forest, and is currently being altered by large-scale agriculture (Fearnside, 2001a; Gibbs *et al.*, 2010), industrial logging (Asner *et al.*, 2005), proliferating roads (Laurance *et al.*, 2001a; Fearnside, 2002, 2007; Killeen, 2007), increasing biofuel production (Butler & Laurance, 2009), hydroelectric dams (Fearnside, 2016a) and oil, gas and mining developments (Finer *et al.*, 2008).

Large expanses of the Amazon have already been cleared, resulting in considerable fragmentation. By the early 1990s, the area of forest that was fragmented (<100 km^2) or vulnerable to edge effects (<1 km from edge) was over 150% greater than the area that had been deforested (Skole & Tucker, 1993). From 1999 to 2002, deforestation and industrial selective logging in Brazilian Amazonia, respectively, created ~32,000 and ~38,000 km of new forest edge annually (Broadbent *et al.*, 2008). Prevailing land uses in Amazonia, such as cattle ranching and small-scale farming, typically produce landscapes dominated by small (<400 ha) and irregularly shaped forest fragments (Fig. 2)(Cochrane & Laurance, 2002; Broadbent *et al.*, 2008). Such fragments are especially vulnerable to a wide array of edge effects and other external vicissitudes (Bierregaard *et al.*, 1992; Laurance *et al.*, 2002, 2011).

Changes in forest cover can have important effects on local climate and vegetation. Habitat fragmentation can promote forest desiccation via phenomena such as the "vegetation breeze" (Fig. 3). This occurs because fragmentation leads to the juxtaposition of cleared and forested lands, which differ greatly in their physical characteristics. Air above forests is cooled by evaporation and especially plant evapotranspiration, but such cooling is greatly reduced above clearings (Avissar & Schmidt, 1998). As a result, the air above clearings heats up and rises, reducing local air pressure and drawing moist air from the surrounding forests into the clearing. As the rising air cools, its moisture condenses into convective clouds that can produce rainfall over the clearing (Avissar & Liu, 1996). The air is then recycled—as cool, dry air—back over the forest. In this way, clearings of a few hundred hectares or more can draw moisture away from nearby forests (Laurance, 2004a; Cochrane & Laurance, 2008; Nobre *et al.*, 2016). In eastern Amazonia, satellite observations of canopy-water content suggest such desiccating effects can penetrate from 1.0-2.7 km into fragmented forests (Briant *et al.*, 2010). This moisture-robbing function of clearings, in concert with frequent burning in adjoining pastures, could help to explain why fragmented forests are so vulnerable to destructive, edge-related fires (Cochrane & Laurance, 2002, 2008; Barlow *et al.*, 2006).

(2) Regional-scale phenomena

Extensive forest clearing reduces the rate of evapotranspiration because pasture grasses and croplands have far less leaf area and shallower roots than do rainforests (Jipp *et al.,* 1998). At regional scales, declining evapotranspiration could reduce rainfall and cloud cover and increase albedo and soil-surface temperatures. Moisture recycling via evapotranspiration is exceptionally important in the hydrological regime of the Amazon (Salati & Vose, 1984; Eltahir & Bras, 1994), especially during the dry season (Malhi *et al.*, 2008), because the forest is both vast and far from the nearest ocean.

However, the regional consequences of large-scale deforestation are far from fully understood. Some modeling studies suggest that Amazonian deforestation could reduce basin-wide precipitation by roughly 20-30%, but these estimates rely on a simplistic assumption of complete, uniform forest clearing (e.g. Nobre *et al.*, 1991; Dickinson & Kennedy, 1992; Lean & Rowntree, 1993). Model results based on actual (circa 1988) deforestation patterns in Brazilian Amazonia have been less dramatic, with deforested regions predicted to experience modest (6-8%) declines in rainfall, moderate (18-33%) reductions in evapotranspiration, higher soil-surface temperatures and greater windspeeds (from reduced surface drag), which could affect moisture convergence and circulation (Walker *et al.*, 1995; Sud *et al.*, 1996). It is even possible that moderate forest loss and fragmentation could *increase* net regional precipitation in the near term, as a result of increasing convectional storms driven by vegetation breezes, although the main effect would be to remove moisture from forests and redistribute it over adjoining clearings. The greatest concern is that if deforestation reaches some critical threshold (see below), Amazonian rainfall might decline abruptly as the regional hydrological system collapses (Avissar *et al.*, 2002; Nobre *et al.*, 2016).

Massive smoke plumes produced by forest and pasture fires cause two additional effects of forest loss. Smoke hypersaturates the atmosphere with cloud condensation nuclei (microscopic particles in aerosol form) that bind with airborne water molecules and thereby inhibit the formation of raindrops (Rosenfeld, 1999). In addition, by absorbing solar radiation, smoke plumes warm the atmosphere, inhibiting cloud formation. As a result of these two effects, large fires can create rain shadows that extend for hundreds or even thousands of kilometers downwind (Freitas *et al.*, 2000). This can be a serious threat to forests because tropical fires are lit during the critical dry-season months, when plants are already moisture stressed and most vulnerable to fire.

(3) Global-change phenomena

How will global-change drivers affect the Amazon? Although model predictions for future climates in Amazonia vary considerably, it is generally expected that parts of the basin will become hotter and drier under projected global warming (IPCC, 2013; Nobre *et al.*, 2016). What this portends for the Amazon is a matter of some controversy. Earlier studies assuming CO_2 concentrations about twice those in the pre-industrial atmosphere, notably by the UK Hadley Centre, projected disastrous forest die-offs (Cox *et al.*, 2000, 2004). However, this conclusion has now been countered by new models from the same research group, suggesting the Amazon forest will remain almost entirely intact at up to four times pre-industrial CO_2 levels (Cox *et al.*, 2013; Good *et al.*, 2013; Huntingford *et al.*, 2013). The main difference is that the newer models include CO_2-fertilization effects (Kimball *et al.*, 1993), which are assumed to increase plant growth and water-use efficiency. This is because the higher atmospheric CO_2 concentration should allow plants to conserve water by decreasing the duration of stomatal-opening periods while still taking in adequate CO_2 for photosynthesis.

Other global-change phenomena, such as extreme climatic events, could also potentially have important impacts. For instance, droughts in the Amazon are normally associated with El Niño events and are strongest in the southern, eastern and north-central Amazon—areas of the basin that already experience pronounced dry seasons. However, severe droughts in 2005 and 2010 arose from a completely different cause—exceptionally high Atlantic sea-surface temperatures, which caused the rain-bearing inter-tropical convergence zone to shift northward (Lewis *et al.*, 2011). The resulting droughts affected not just the drier, more seasonal parts of the basin but also its wettest areas in central and western Amazonia. Because plant species in these wet areas are adapted to perennially humid conditions, the new droughts caused massive plant mortality, killing tens of millions of trees while releasing several billion tonnes of atmospheric carbon emissions (Lewis *et al.*, 2011;

250 Marengo *et al.*, 2012). With mounting evidence that climatic extremes could become more
251 frequent and intense in a warming world (Vera *et al.*, 2006; Herring *et al.*, 2015; Jiménez-
252 Muñoz *et al.*, 2016), could the Amazon be driven into a new kind of climatic dynamic—one
253 for which its ecosystems and biodiversity are poorly adapted?
254
255 **III. STUDY AREA AND KEY DATASETS**
256 **(1) Study area**
257 The experimental landscape of the BDFFP spans ~1000 km^2 in area and is located 80 km
258 north of Manaus, Brazil. The topography is relatively flat (80-160 m elevation) but dissected
259 by numerous stream gullies. The heavily weathered, nutrient-poor soils of the study area are
260 typical of large expanses of the Amazon Basin. Rainfall ranges from 1900 to 3500 mm
261 annually with a moderately strong dry season from June to October. The forest canopy is 30-
262 37 m tall, with emergent trees to 55 m. Species richness of trees (≥10 cm diameter at breast
263 height) often exceeds 280 species ha^{-1}, which is among the highest known tree diversity in the
264 world (Oliveira & Mori, 1999; S. G. Laurance *et al.*, 2010b). Comparably high levels of
265 diversity are seen in many other plant and animal taxa.
266 The study area includes three large cattle ranches (~5000 ha each) containing 11 forest
267 fragments (five of 1 ha, four of 10 ha and two of 100 ha), and large expanses of nearby
268 continuous forest that serve as experimental controls (Fig. 1). In the early 1980s, the
269 fragments were isolated from nearby intact forest by distances of 80-650 m through clearing
270 and burning of the surrounding forest. A key advantage was that pre-fragmentation censuses
271 were conducted for many animal and plant groups (e.g. trees, understory birds, small
272 mammals, primates, frogs, many invertebrate taxa), thereby allowing long-term changes in
273 these groups to be assessed far more confidently than in most other fragmentation studies.
274 Because of poor soils and low productivity, the ranches surrounding the BDFFP

fragments were largely abandoned, especially after government fiscal incentives dried up from 1988 onwards. Secondary forests—initially dominated by *Vismia* spp. in areas that were cleared and burned, and by *Cecropia* spp. in areas that were cleared without fire—proliferated in many formerly forested areas (Mesquita *et al.*, 2001). Some regenerating areas initially dominated by *Cecropia* later grew into structurally complex (>20 m tall), species-rich secondary forests (Longworth *et al.*, 2014). *Vismia*-dominated regrowth, however, which is relatively species poor, is maturing far more slowly (Norden *et al.*, 2011; Williamson *et al.*, 2014).

To help maintain isolation of the experimental fragments, 100 m-wide strips of regrowth were cleared and burned around each fragment on 4-5 occasions, most recently in 2013-2014. However, human disturbances that affect many fragmented landscapes in the Amazon, such as major fires, logging and hunting (Michalski & Peres, 2005), are largely prevented at the BDFFP.

(2) Unique datasets

The BDFFP sustains some of the longest-running and highest-quality environmental datasets in the Amazon. This includes a network of 69 1-ha forest-dynamics plots arrayed across intact and fragmented forests in the study area, which has been monitored since the early 1980s, and a permanent 25-ha plot in intact forest established in 2005. These plots have made important contributions to reducing uncertainties in biomass and carbon-storage estimates for the Amazon (e.g. Phillips *et al.*, 1998; Baker *et al.*, 2004; Nascimento & Laurance, 2002). For example, in comparison to the 3000 1-ha plots surveyed by the RADAMBRASIL Project (Nogueira *et al.*, 2008, 2015), the BDFFP plots include data on nearly all other forest components such as smaller (1-30 cm diameter) trees, palms, lianas, strangler figs, understory vegetation and dead biomass (Nascimento & Laurance, 2002, 2004). These data allow one to

assess spatial variability in aboveground biomass with a high degree of confidence. For example, the aboveground biomass of trees varies considerably among the 69 1-ha plots in the BDFFP landscape (mean ± SD = 356 ± 47 Mg ha^{-1}; Laurance *et al.*, 1999). This high variability demonstrates a need for many plots that are spatially stratified, rather than only a few plots of 1 ha or smaller scattered irregularly around the Amazon, for calibrating satellite imagery for biomass mapping, and for estimating greenhouse-gas emissions from ongoing deforestation (see Fearnside, 2016b).

Floristic data from the BDFFP are exceptional for their high quality of species identifications, allowing better matching with plant functional and phylogenetic traits such as wood density and tree form (e.g., Fearnside, 1997; Nogueira *et al.*, 2005, 2007; Chave *et al.*, 2006; Souza *et al.*, 2016). Given their broad spatial extent and temporal depth, these data have also contributed to knowledge of the diversity of Amazonian plant species and their relationships to soil texture and chemistry, topography, forest dynamics and climatic variables at both landscape and regional scales (e.g. Bohlman *et al.*, 2008; S. G. Laurance *et al.*, 2009, 2010a, 2010b; ter Steege *et al.*, 2013). Biodiversity and ecosystem processes represent part of what is lost when the forest is destroyed or degraded. Understanding these processes is essential for assessing not only the vulnerability of forests, but also their potential resilience in the face of global change and their rates of recovery following various perturbations (Williamson *et al.*, 2014; Souza *et al.*, 2016). Datasets for a number of faunal groups, such as birds, amphibians, primates and major invertebrate taxa, are of comparable quality and duration.

IV. CHANGES IN INTACT FORESTS

(1) Unexpected trends

As part of its original mission to assess long-term changes in fragmented forests, the BDFFP has two types of experimental controls (Lovejoy *et al.*, 1986; Bierregaard *et al.*, 1992). The first is that standardized censuses of many plant and animal taxa were conducted in each experimental fragment before it was isolated from the surrounding forest. The second is that dozens of 'control' sites in nearby intact forests have been monitored for up to 38 years, to assess the temporal dynamics of these sites. The intact-forest sites were expected to vary randomly over time or respond to occasional vicissitudes such as droughts, but not to change over time in a directional manner.

A major surprise, however, is that the BDFFP controls have changed in several concerted ways (Laurance *et al.*, 2014b). Before interpreting how fragmentation has altered ecological communities in the BDFFP, it is first important to identify how the intact-forest sites have changed—as these widespread effects are presumably altering the forest fragments as well. The long-term monitoring of tens of thousands of trees and populations of many other plant and animal groups has allowed researchers to identify synchronous changes in the undisturbed forests at the intact sites—and to attempt to infer their environmental causes.

How have the intact forests changed? Over the past 2-3 decades, we have found that (1) forest dynamics (tree mortality and recruitment) have accelerated significantly over time (Laurance *et al.,* 2004a, 2014b; S. G. Laurance *et al.,* 2009); (2) tree-community composition has shifted, generally in favor of faster-growing canopy trees and against shade-tolerant subcanopy trees (Laurance *et al.,* 2004a, 2005); (3) growth rates have increased for the large majority (84%) of tree genera in our study area (Fig. 4)(Laurance *et al.,* 2004a); (4) aboveground tree biomass has increased significantly over time (although tree-stem numbers have not changed significantly; S. G. Laurance *et al.*, 2009); and (5) lianas have increased markedly in abundance (Fig. 5)(Laurance *et al.* 2014a, 2014b).

(2) Potential environmental drivers

Why are the intact forests changing? The causes of such changes are incompletely understood (Lewis *et al.,* 2004a, 2009a) and often controversial (Clark, 2004; Fearnside 2004). Nonetheless, the trends we detected appear broadly consistent with those observed elsewhere in many Amazonian (Phillips & Gentry, 1994; Phillips *et al.,* 1998, 2002; Baker *et al.,* 2004; Lewis *et al.,* 2004b; Schnitzer & Bongers, 2011) and African (Lewis *et al.*, 2009a) tropical forests. These trends are consistent with ecological patterns expected from rising forest productivity—including faster plant growth, increasing forest biomass, intensifying competition leading to greater plant mortality and turnover, and increasing abundances of plant species that can attain high growth rates or are advantaged in dynamic forests (Laurance *et al.,* 2004a; Lewis *et al.,* 2004b, 2009a).

The most frequently invoked driver of rising tropical forest productivity is CO_2 fertilization (e.g. Lewis *et al.*, 2004a, 2009b), presumably because many plants show faster growth under enriched CO_2 (Oberbauer *et al.,* 1985; Granados & Körner, 2002; Körner 2004) and because atmospheric CO_2 levels have risen rapidly, especially in recent decades. This view is supported by compelling evidence of a large carbon sink in the biosphere (Ballantyne *et al.*, 2013), a substantial part of which appears to be on land (Sarmiento *et al.,* 2010) and in the tropics (Lewis *et al.,* 2009b; Huntingford *et al.,* 2013).

Other explanations for the rising productivity, however, are not implausible. For instance, droughts can influence forest dynamics and composition and appear to be increasing in parts of the Amazon (Lewis *et al.,* 2009b; Marengo *et al.*, 2011; Chou *et al.*, 2013; Fu *et al.,* 2013). The increase in forest dynamics we observed in intact forests appears to be driven primarily by rising tree mortality, with recruitment and growth often lagging behind periods of high mortality. These mortality pulses are positively associated with several factors, including El Niño droughts and increasing rainfall seasonality (S. G. Laurance *et al.*, 2009).

374 Additionally, multi-decadal shifts in solar radiation or cloudiness could potentially
375 increase forest productivity, although evidence for such shifts in the tropics is limited (Lewis
376 *et al.,* 2009b). Recovery from past disturbance has also been hypothesized to underlay
377 changes at some tropical forest sites, but there is no evidence of widespread disturbance in our
378 study area (Laurance *et al.,* 2004a, 2005) aside from charcoal fragments that are at least four
379 centuries old (Bassini & Becker, 1990; Fearnside & Leal Filho, 2001), possibly indicating
380 major fires during past mega-El Niño events (Meggers, 1994).
381 The notable increases in liana abundance in our intact forests (Laurance *et al.,* 2014a)
382 might arise because lianas appear to exploit rising CO_2 concentrations and drier conditions
383 more effectively than do trees (Condon *et al.*, 1992; Granados & Körner, 2002; but see
384 Marvin *et al.,* 2015). Trees with heavy liana infestations are known to exhibit elevated
385 mortality and reduced growth (Ingwell *et al.*, 2010). Notably, in our study area, liana
386 abundance is strongly and negatively correlated with live tree biomass (Fig. 6)(Laurance *et*
387 *al.*, 2001b). Liana increases over time have also been observed in tropical forests in western
388 Amazonia, the Guianas, Central America and elsewhere (Schnitzer & Bongers, 2011), with
389 rising atmospheric CO_2 and possibly increasing drought being the most frequent explanations
390 (see Laurance *et al.*, 2014a and references therein). This potentially negative effect of CO_2
391 enrichment on forest biomass via increasing liana infestations is not included in the latest
392 Hadley Centre models (Cox *et al.*, 2013; Good *et al.*, 2013; Huntingford *et al.*, 2013), and
393 could cancel out some of the carbon-storage benefits suggested for a high-CO_2 future (Körner,
394 2004, 2017).
395 Hence, for whatever the reason or reasons, it is apparent that the intact forests in our
396 study area are changing in a variety of ways. Such changes are likely to interact with, and
397 potentially complicate or amplify, the impacts of fragmentation on tropical forest
398 communities.

V. CONSEQUENCES OF FRAGMENT SIZE

The BDFFP's original mission focuses on assessing the effects of fragment area on Amazonian forests and fauna, and on key ecological and ecosystem processes. Here we summarize major findings and conservation lessons that have been gleaned to date.

(1) Sample effects

Many species in Amazonian forests are rare or patchily distributed. This phenomenon is especially pronounced in the large expanses of the basin that overlay heavily weathered, nutrient-poor soils (e.g. Radtke *et al.*, 2008). In such areas resources such as fruits, flowers and nectar are typically scarce and plants are heavily defended against herbivore attack (Laurance, 2001).

Herein lies a key implication for understanding forest fragmentation: given their rarity, many species may be absent from fragments not because their populations have vanished, but because they were simply not present at the time of fragment creation—a phenomenon termed the 'sample effect' (Wilcox & Murphy, 1985). Such sample effects are the hypothesized explanation for the absence of many rare understory bird species from fragments (Ferraz *et al.*, 2007). In addition, many beetles (Didham *et al.*, 1998a), bats (Sampaio, e*t al.*, 2003; Farneda *et al.*, 2015; Meyer *et al.*, 2015; Rocha *et al.*, 2016), ant-defended plants (Bruna, *et al.*, 2005) and trees (Bohlman *et al.*, 2008; Laurance *et al.*, 2010b) at the BDFFP exhibit high levels of rarity, habitat specialization or patchiness.

(2) Area effects

Understanding fragment-area effects has long been a central goal of the BDFFP (Lovejoy & Oren, 1981; Lovejoy *et al.*, 1984, 1986; Pimm, 1998). The species richness of many

organisms declines with decreasing fragment area, even with constant sampling effort across all fragments. Such declines are evident in leaf bryophytes (Zartman, 2003), tree seedlings (Benítez-Malvido & Martinez-Ramos, 2003a), palms (Scariot, 1999), understory insectivorous birds (Stratford & Stouffer, 1999; Ferraz *et al.*, 2007), bats (Sampaio, 2000; Rocha *et al.*, 2016), primates (Gilbert & Setz, 2001; Boyle & Smith, 2010a) and larger herbivorous mammals (Timo 2003), among others. For such groups, smaller fragments (<100 ha) are often unable to support viable populations. A few groups, such as ant-defended plants and their ant mutualists, show no significant decline in diversity with fragment area (Bruna, *et al.*, 2005).

Fragment size also influences the rate of species losses, with smaller fragments losing species more quickly (Lovejoy *et al.*, 1986; Stouffer *et al.*, 2008). Assuming that the surrounding matrix is hostile to bird movements and precludes colonization, Ferraz *et al.* (2003) estimated that a 1000-fold increase in fragment area would be needed to slow the rate of local species extinctions by 10-fold. Even a fragment of 10,000 ha in area would be expected to lose a substantial part of its bird fauna within one century (Ferraz *et al.*, 2003). Similarly, long-term mark-recapture studies suggest that very large fragments will be needed to maintain fully intact assemblages of certain faunal groups, such as ant-following birds, which forage over large areas of forest (Van Houtan *et al.*, 2007).

VI. EDGE EFFECTS

An important insight from the BDFFP is the extent to which edge effects—physical and biotic changes associated with the abrupt, artificial margins of habitat fragments—influence the dynamics and composition of plant and animal communities. Here we summarize key findings from this work.

(1) Forest hydrology

The hydrological regimes of fragmented landscapes differ markedly from those of intact forest (Kapos, 1989; Kapos *et al.*, 1993). Pastures or crops surrounding fragments have much lower rates of evapotranspiration than do forests, causing such areas to be hotter and drier than forests (Camargo & Kapos, 1995). Field observations and heat-flux simulations suggest that desiccating conditions can penetrate up to 100-200 m into fragments from adjoining clearings (Malcolm, 1998; Didham & Lawton, 1999). Further, streams in fragmented landscapes experience greater temporal variation in flow rate than do those in forests, because clearings surrounding fragments have less evapotranspiration and rainfall interception and absorption by vegetation (Trancoso, 2008). Rapid runoff promotes localized flooding in the wet season and stream failure in the dry season, with potentially important impacts on aquatic invertebrates (Nessimian *et al.*, 2008) and fish assemblages.

(2) Striking diversity of edge effects

At least over the first 3-4 decades after isolation, edge effects have been among the most important drivers of ecological change in the BDFFP fragments. The distance to which different edge effects penetrate into fragments varies widely, ranging from 10-300 m at the BDFFP (Laurance *et al.*, 2002) and considerably further (at least 2-3 km) in areas of the Amazon where edge-related fires are common (Cochrane & Laurance, 2002, 2008; Briant *et al.*, 2010).

Edge phenomena are remarkably diverse (Fig. 7). They include increased desiccation stress, wind shear and wind turbulence that sharply elevate rates of tree mortality and damage (Laurance *et al.*, 1997, 1998a). These in turn cause wide-ranging alterations in the community composition of trees (Laurance *et al.*, 2000, 2006a, 2006b) and lianas (Laurance *et al.*, 2001b). Such stresses may also reduce germination (Bruna 1999) and establishment (Uriarte

474 *et al.*, 2010) of shade-tolerant plant species in fragments, leading to dramatic changes in the
475 composition and abundance of tree seedlings (Benítez-Malvido, 1998; Benítez-Malvido &
476 Martinez-Ramos, 2003a).

477 Many animal groups, such as numerous bees, wasps, flies (Fowler *et al.*, 1993),
478 beetles (Didham *et al.*, 1998a, 1998b), ants (Carvalho & Vasconcelos, 1999), butterflies
479 (Brown & Hutchings, 1997), understory birds (Quintela, 1985; S. G. Laurance, 2004) and
480 gleaning predatory bats (Rocha, 2016; Rocha *et al.*, 2016), decline in abundance near forest
481 edges. Edge habitats of continuous forest and larger fragments (100 ha) have fewer species of
482 bats and higher levels of dominance by a few common species (Rocha, 2016; Rocha *et al.*,
483 2016). Negative edge effects are apparent even along narrow forest roads (20-30 m width).
484 Among understory birds, for example, five of eight foraging guilds declined significantly in
485 abundance within 70 m of narrow roads, evidently in response to increased light and forest
486 disturbance near road edges (Laurance, 2004b).

487 Some groups of organisms remain stable or even increase in abundance near edges.
488 Leaf bryophytes (Zartman & Nascimento, 2006), wandering spiders (*Ctenus* spp; Rego *et al.*,
489 2007; Mestre & Gasnier, 2008) and many frogs (Gascon, 1993) displayed no significant
490 response to edges. Organisms that favor forest ecotones or disturbances, such as many species
491 of gap-favoring and frugivorous birds (Laurance, 2004b), hummingbirds (Stouffer &
492 Bierregaard, 1995a), frugivorous bats that exploit early successional plants (Sampaio, 2000,
493 Rocha *et al.*, 2016), light-loving butterflies (Leidner *et al.*, 2010) and fast-growing lianas
494 (Laurance *et al.*, 2001b), increase in abundance near edges, sometimes dramatically.
495

496 **(3) Impacts of multiple edges**

497 BDFFP research demonstrates that plots near two or more edges suffer more severe edge
498 effects than do those near just one edge (Fig. 8). This conclusion is supported by studies of

499 edge-related changes in forest microclimate (Kapos, 1989; Malcolm, 1998), vegetation
500 structure (Malcolm 1994), tree mortality (Laurance *et al.*, 2006a), abundance and species
501 richness of tree seedlings (Benítez-Malvido, 1998; Benítez-Malvido & Martinez-Ramos,
502 2003a), liana abundance (Laurance *et al.*, 2001b) and the density and diversity of disturbance-
503 loving pioneer trees (Laurance *et al.*, 2006a, 2006b, 2007). The additive effects of nearby
504 edges probably help to explain why small (<10 ha) or irregularly shaped forest remnants are
505 often so severely altered by forest fragmentation (Zartman, 2003; Laurance *et al.*, 2006a).
506 Some fauna are likewise sensitive to multiple edges. For instance, the number of nearby forest
507 edges was found to be an important predictor of local bat abundance (Rocha *et al.*, 2016).
508
509 **(4) Effects of edge age and adjoining vegetation**
510 When a forest edge is newly created, it is open to fluxes of wind, heat and light, creating
511 sharp edge-interior gradients in forest microclimate that stress or kill many rainforest trees
512 (Lovejoy *et al.*, 1986; Sizer & Tanner, 1999). As the edge ages, however, proliferating vines
513 and lateral branch growth tend to 'seal' the edge, making it less permeable to microclimatic
514 changes (Camargo & Kapos, 1995; Didham & Lawton, 1999). Tree death from microclimatic
515 stress is likely to decline over the first few years after edge creation (D'Angelo *et al.*, 2004) as
516 the edge becomes less permeable, because many drought-sensitive individuals die
517 immediately and because surviving trees may acclimate to drier, hotter conditions near the
518 edge (Laurance *et al.*, 2006a). Tree mortality from wind turbulence, however, probably
519 increases as the edge ages and becomes more closed because, as suggested by wind-tunnel
520 models, downwind turbulence increases if edges are less permeable (Laurance, 2004a).
521 Regrowth forest adjoining fragment edges can also lessen edge-effect intensity.
522 Microclimatic changes (Didham & Lawton, 1999), tree mortality (Mesquita *et al.*, 1999) and
523 edge avoidance by understory birds (Develey & Stouffer, 2001; Laurance, 2004b, S. G.

524 Laurance *et al.*, 2004) and gleaning animal-eating bats (Sampaio, 2000; Meyer *et al.*, 2016;
525 Rocha, 2016; Rocha *et al.*, 2016) are all reduced when forest edges are buffered by adjoining
526 regrowth forest, relative to edges bordered by cattle pastures. Mature regrowth can be
527 particularly benign for some fauna; for example, diverse assemblages of aerial-feeding
528 insectivorous bats showed similar activity patterns in primary forest and in adjoining 30-year-
529 old secondary forests (Navarro, 2014).
530
531 **VII. FOREST ISOLATION AND THE MATRIX**
532 Unlike true islands encircled by water, habitat fragments are surrounded by a matrix of
533 modified vegetation that can be highly variable in space and time. Here we highlight key
534 factors that can influence the matrix and how, in turn, the matrix influences fragment
535 dynamics and composition.
536
537 **(1) Matrix structure and composition**
538 The BDFFP landscape has experienced considerable dynamism over time. In particular,
539 secondary forests have gradually overgrown most pastures in the study area. This regrowth
540 lessens the effects of fragmentation for some species, with the matrix becoming less hostile to
541 faunal use and movements. Several species of insectivorous birds that had formerly
542 disappeared from fragments have recolonized them as surrounding secondary forests
543 regenerated (Stouffer & Bierregaard, 1995b; Stouffer *et al.*, 2011). The rate of local
544 extinctions of birds has also declined (Stouffer *et al.*, 2008).
545 The regenerating forest in the matrix now permits fragments as small as 100 ha to
546 support bird and bat assemblages similar to those in continuous forest (Wolfe *et al.*, 2015;
547 Rocha *et al.*, 2016). For bats, matrix recovery has resulted in marked compositional changes
548 in fragments and shifts in the rank order of the most abundant species (Meyer *et al.*, 2016;

549 Rocha, 2016). Gleaning animal-eating bats, which formerly occurred at low abundances in
550 fragments (Sampaio, 2000) and young regrowth (Bobrowiec & Gribel, 2010), have increased
551 over the past 10-15 years as the surrounding regrowth has expanded and matured (Meyer *et*
552 *al.*, 2016; Rocha, 2016; Rocha *et al.*, 2016). A number of other species, including certain
553 forest spiders (Mestre & Gasnier, 2008), dung beetles (Quintero & Roslin, 2005), euglossine
554 bees (Becker *et al.*, 1991) and monkeys such as red howlers, bearded sakis and brown
555 capuchins (Boyle & Smith, 2010a), have also recolonized some of the fragments.
556 The surrounding matrix also has a strong effect on plant communities in fragments by
557 reducing edge effects (see above), influencing the movements of pollinators (Dick, 2001;
558 Dick *et al.*, 2003) and seed dispersers (Jorge, 2008; Bobrowiec & Gribel, 2010; Boyle &
559 Smith, 2010a) and strongly influencing the seed rain that arrives in fragments. For instance,
560 pioneer trees regenerating in fragments differed strikingly in composition between fragments
561 surrounded by *Cecropia*-dominated regrowth and those encircled by *Vismia*-dominated
562 regrowth (Nascimento *et al.*, 2006). In this way plant and animal communities in fragments
563 may increasingly tend to mirror the composition of the surrounding matrix (Laurance *et al.*,
564 2006a, 2006b), a phenomenon observed elsewhere in the tropics (Janzen, 1983; Diamond *et*
565 *al.*, 1987; Laurance, 1991).
566
567 **(2) Factors influencing the matrix**
568 Land-use history is a key driver of secondary succession in Amazonia, resulting in distinct
569 trajectories of regeneration that differ in structure, composition, biomass and dynamics
570 (Mesquita *et al.*, 1999; Williamson *et al.*, 2014). The recurring use of fire to maintain pastures
571 reduces regenerative potential, leaving lands dominated by scrubby trees in the genus *Vismia*,
572 which are prodigious resprouters that stall succession by inhibiting growth of other tree
573 species (Jakovac *et al.*, 2015). Compared to slash-and-burn agriculture, vegetation biomass

574 recovers much more slowly in lands previously used as pasture, which is currently the
575 predominant land use in Amazonia (Wandelli & Fearnside, 2015). However, where land and
576 fire use has been less intensive, a more diverse vegetation dominated by the genus *Cecropia*
577 fosters relatively rapid plant succession (Longworth *et al.*, 2014).

578 In regenerating forests, plant density and species diversity both decline with distance
579 from primary forest, and also differ between *Vismia*- and *Cecropia*-dominated regrowth.
580 These differences were initially attributed to differential seed-dispersal limitations (Mesquita
581 *et al.*, 2001; Puerta, 2002). However, it now appears that the seed rains are similar in both
582 types of regrowth and are strongly dominated by pioneer species (Wieland *et al.*, 2011). This
583 suggests that birds and bats, the primary seed dispersers, are feeding mainly in regrowth and
584 rarely transporting primary-forest seeds into the regrowth. Instead, the legacy of past land use
585 endures as abandoned pastures—especially those dominated by *Vismia*—remain depauperate
586 for at least a quarter of a century (Massoca *et al.*, 2013; Mesquita *et al.*, 2015).

587

588 **(3) Narrow forest clearings**

589 Many Amazonian species avoid forest clearings, even those that are surprisingly narrow. A
590 number of understory insectivorous birds exhibit depressed abundances near roads of just 20-
591 40 m width (S. G. Laurance, 2004b) and their rate of movements across those roads is
592 strongly reduced (S. G. Laurance *et al.*, 2004). Experimental translocations of resident adult
593 birds reveal that such species can be compelled to cross a highway (50-75 m width) but not a
594 small pasture (250 m width) to return to their territory (Laurance & Gomez, 2005).
595 Individuals of some other vulnerable bird species, however, have traversed clearings to escape
596 from small fragments to larger forest areas (Harper, 1989; Van Houtan *et al.*, 2007). Captures
597 of understory birds declined dramatically in fragments when a 100 m-wide swath of regrowth
598 forest was cleared around them, suggesting that species willing to traverse regrowth had a

599 strong aversion to such clearings (Stouffer *et al.*, 2006).

600 Aside from birds, clearings of just 100-200 m width can evidently reduce or halt the
601 movements of many forest-dependent organisms (Laurance *et al.*, 2009), ranging from
602 herbivorous insects (Fáveri *et al.*, 2008), euglossine bees (Powell & Powell, 1987) and dung
603 beetles (Klein, 1989) to the spores of epiphyllous lichens (Zartman & Nascimento, 2006;
604 Zartman & Shaw, 2006). Narrow clearings can also provide invasion corridors into forests for
605 exotic and non-forest species (Gascon *et al.*, 1999; Laurance *et al.*, 2009).
606

607 **VIII. DYNAMICS OF FOREST FRAGMENTS**

608 Here we highlight some factors that can influence the dynamics of Amazonian forest
609 fragments and the unusual ecological communities than can arise as a consequence.
610

611 **(1) Rare disturbances**

612 Rare events such as droughts, local flooding and windstorms have strongly influenced the
613 ecology of BDFFP fragments. Rates of tree mortality rose abruptly in both fragmented
614 (Laurance *et al.*, 2001c) and intact forests (Williamson *et al.*, 2000) in the year after the
615 intense 1997 El Niño drought and heavy 1998 La Niña rains. Such pulses of tree death can
616 drive changes in the floristic composition and carbon storage of fragments (Laurance *et al.*,
617 2007). Leaf-shedding by drought-stressed trees also increases markedly during droughts,
618 especially within ~60 m of forest edges, increasing the quantity of leaf litter on the forest floor
619 (Laurance & Williamson, 2001). Such dense litter elevates the susceptibility of fragments to
620 intrusion by destructive surface fires (Cochrane & Laurance, 2002, 2008) and can slow forest
621 regeneration by suppressing seed germination and seedling establishment (Bentos *et al.*,
622 2013). Local flooding caused tree mortality in one of our plots to rise five-fold (S. G.
623 Laurance *et al.*, 2009), a pattern also observed in other low-lying plateaus and microsites in

624 the BDFFP study area (Mori & Becker, 1991).

625 Intense windblasts from convectional thunderstorms have occasionally flattened parts
626 of the BDFFP landscape and caused intense forest damage and tree mortality, especially in
627 the fragments. Fragments in the easternmost cattle ranch at the BDFFP have had substantially
628 lower rates of tree mortality than those in the other two ranches (Fig. 1), because the former
629 have so far escaped major windstorms (Laurance *et al.*, 2007). These differences have
630 strongly influenced the rate and trajectory of change in tree-community composition in
631 fragments (Laurance *et al.*, 2006b). Hence, by altering forest dynamics, composition,
632 structure and carbon storage, rare disturbances have left an enduring imprint on the ecology of
633 fragmented forests.

634

635 **(2) Hyperdynamism**

636 Relative to intact forest, the BDFFP fragments experience exceptional variability in
637 population and community dynamics, despite being largely protected from ancillary human
638 threats such as fires, logging and overhunting. Having a small resource base, a habitat
639 fragment is inherently vulnerable to stochastic effects and external vicissitudes. Species
640 abundances can thus fluctuate dramatically in small communities, especially when
641 immigration is low and disturbances are frequent (Hubbell, 2001). Edge effects, reduced
642 dispersal, external disturbances and changing herbivore or predation pressure can all elevate
643 the dynamics of plant and animal populations in fragments (Laurance, 2002, 2008).

644 Many examples of hyperdynamism have been observed in the BDFFP fragments.
645 Some butterfly species have experienced dramatic population irruptions in response to a
646 proliferation of their favored host plants along fragment margins (Brown & Hutchings, 1997),
647 and butterfly communities in general are hyperdynamic in fragments (Fig. 9)(Leidner *et al.*,
648 2010). Bat assemblages also show atypically high species turnover (Meyer *et al.*, 2016), as do

649 understory birds (Stouffer *et al.*, 2008, 2011), especially in smaller fragments. Streamflows
650 are far more variable in fragmented than forested watersheds (Trancoso, 2008). Rates of tree
651 mortality and recruitment are chronically elevated in fragments (Laurance *et al.*, 1998a,
652 1998b), with major mortality pulses associated with rare disturbances (see above). These
653 pulses of tree death followed by accelerated recruitment of young trees lead to large
654 fluctuations in the number of trees per plot (Fig. 10). Further, tree species disappear and turn
655 over far more rapidly in fragments than intact forest, especially within ~100 m of forest
656 margins (Laurance *et al.*, 2006b). These and many other instabilities plague small, dwindling
657 populations in the BDFFP fragments.
658
659 **(3) Diverging trajectories of fragments**
660 A key insight from our long-term experiment is that different fragmented landscapes— even
661 those as alike as the three large cattle ranches in the BDFFP, which have very similar forests,
662 soils, climate, fragment ages and land-use histories—can diverge to a surprising degree in
663 species composition and dynamics. Although spanning just a few dozen kilometers, the three
664 ranches are following unexpectedly different trajectories of change.
665 At the outset, small initial differences among the ranches multiplied into much bigger
666 differences. Parts of the western and eastern ranches were cleared in 1983, when an early wet
667 season prevented burning of the felled forest. Tall, floristically diverse *Cecropia*-dominated
668 regrowth quickly developed in these areas, whereas areas cleared with fire in the years just
669 before or after became cattle pastures or, eventually, scrubby *Vismia*-dominated regrowth
670 (Williamson & Mesquita, 2001). For example, these different successional trajectories led to
671 distinct bat assemblages: *Cecropia*-dominated regrowth retained a considerably higher
672 fraction of the forest-specialist bat species found in continuous forest, compared to *Vismia*
673 regrowth (Bobrowiec & Gribel, 2010). As discussed above, the differing matrix vegetation

674 strongly affected the dynamics of plant and animal communities in the nearby fragments.
675 These differences were magnified by subsequent windstorms, which heavily damaged most
676 fragments in the central and western ranches, yet left fragments in the eastern ranch
677 unscathed. Even identically sized fragments in the three ranches have had remarkably
678 different dynamics and trajectories of compositional change (Laurance *et al.*, 2007).
679 The apparently acute sensitivity of fragments to local landscape and weather dynamics—even
680 within a study area as initially homogeneous as ours—prompted us to propose a "landscape-
681 divergence hypothesis" (Laurance *et al.*, 2007). We argue that fragments within the same
682 landscape will tend to have similar dynamics and trajectories of change in species
683 composition, which will often differ from those in other landscapes. Over time, this process
684 will tend to homogenize fragments within the same landscape, and promote ecological
685 divergence among fragments in different landscapes. Evidence for this hypothesis is provided
686 by tree communities in our fragments, which appear to be diverging in composition among
687 the three cattle ranches (Fig. 11). Pioneer and opportunistic trees are increasing in all
688 fragments, but the composition of these secondary plant species and their rates of increase
689 differ markedly among the three ranches (Scariot, 2001; Laurance *et al.*, 2006a,
690 2007; Nascimento *et al.*, 2006). A similar pattern of biotic divergence is evident in the
691 secondary-forest bat assemblages found at the different ranches (Bobrowiec & Gribel, 2010).
692
693 **(4) Ecological distortions**
694 Many ecological interactions are altered in fragmented landscapes. For instance, in mixed-
695 species bird flocks, interspecific interactions are lower, both in number and frequency, in 10-
696 ha fragments and the secondary forest matrix than in more preserved habitats (continuous
697 forest and 100-ha fragments), resulting in reduced flock cohesion and stability (Mokross *et*
698 *al.*, 2014). Fragmented communities can pass through unstable transitional states that may not

699 otherwise occur in nature (Terborgh *et al.*, 2001; Gibson *et al.*, 2013). Moreover, species at
700 higher trophic levels, such as predators and parasites, are often more vulnerable to
701 fragmentation than are herbivores, thereby altering the structure and functioning of food webs
702 (Didham *et al.*, 1998b; Terborgh et al., 2001).

703 BDFFP findings suggest that even forest fragments that are unhunted, unlogged and
704 unburned have reduced densities of key mammalian seed dispersers. As a result, seed
705 dispersal for the endemic, mammal-dispersed tree *Duckeodendron cestroides* was far lower in
706 fragments, with just ~5% of the number of seeds being dispersed >10 m away from parent
707 trees than in intact forest (Cramer *et al.*, 2007a). Leaf herbivory appears reduced in fragments,
708 possibly because of lower immigration of insect herbivores (Fáveri *et al.*, 2008). Dung beetles
709 exhibit changes in biomass and guild structure in fragments (Radtke *et al.*, 2008) that could
710 alter rates of forest nutrient cycling and secondary seed dispersal (Klein, 1989; Andresen,
711 2003). Exotic Africanized honeybees, a generalist pollinator, are abundant in matrix and edge
712 habitats and can alter pollination success and gene flow for some tree species (Dick, 2001;
713 Dick *et al.*, 2003). A bewildering variety of ecological distortions can pervade fragmented
714 habitats, and a challenge for conservation biologists is to identify those of greatest importance
715 and generality.

716

717 **(5) Forest-carbon dynamics**

718 Habitat fragmentation affects far more than biodiversity and interactions among species;
719 many ecosystem functions, including forest hydrology (see above) and biochemical cycles,
720 are also being altered. Among the most important of these are fundamental alterations in
721 forest biomass and carbon storage.

722 A suite of interrelated changes affects carbon stocks in fragmented forests. Many trees
723 die near forest edges (Laurance *et al.*, 1997, 1998a), including an alarmingly high proportion

724 of large (≥60 cm dbh) canopy and emergent trees that store a large fraction of the total forest
725 carbon (Laurance *et al.*, 2000). Compared to the mature-phase trees they replace, fast-growing
726 pioneer trees and lianas that proliferate in fragments are smaller and have lower wood density
727 and thereby sequester much less carbon (Laurance *et al.*, 2001b, 2006a). Based on current
728 rates of forest fragmentation, the edge-related loss of carbon storage in the tropics could
729 produce tens of millions of tons of atmospheric carbon emissions annually, above and beyond
730 that caused by deforestation per se (Laurance *et al.*, 1998c; Groeneveld *et al.*, 2009).
731 In addition, biomass is being fundamentally redistributed in fragmented forests (Fig.
732 12). Less biomass is stored in large, densely wooded old-growth trees and more in fast-
733 growing pioneer trees, disturbance-loving lianas, woody debris and leaf litter (Sizer *et al.*,
734 2000; Nascimento & Laurance, 2004; Vasconcelos & Luizão, 2004). Soil carbon also
735 increases as the abundant dead biomass in fragments decomposes (Barros & Fearnside, 2016).
736 Finally, carbon cycling accelerates. The large, old-growth trees that predominate in intact
737 forests can live for many centuries or even millennia (Chambers *et al.*, 1998; Laurance *et al.*,
738 2004b), sequestering carbon for long periods of time. However, the residence time of carbon
739 in early successional trees, vines and necromass (wood debris, litter), which proliferate in
740 fragments, is far shorter (Nascimento & Laurance, 2004). Other biochemical cycles, such as
741 those affecting key nutrients such as phosphorus (Sizer *et al.*, 2000) and calcium
742 (Vasconcelos & Luizão, 2004), might also be altered in fragmented forests, given the striking
743 changes in biomass dynamics, hydrology and thermal regimes they experience there.
744

745 **IX. SPECIES RESPONSES TO FRAGMENTATION**

746 Individual species and ecological groups can differ greatly in their responses to habitat
747 fragmentation. Some decline or disappear, others remain roughly stable and yet others
748 increase, sometimes dramatically. Understanding how and why different species vary so

749 dramatically in their responses has been a major goal of conservation researchers. Here we
750 underscore key conclusions from the BDFFP.
751
752 **(1) Non-random extinctions**
753 Local extinctions of species in the BDFFP fragments have occurred in a largely predictable
754 sequence, with certain species being consistently more vulnerable than others. Among birds,
755 various species of understory insectivores, including army ant-followers, solitary species,
756 terrestrial foragers and obligate mixed-flock members, are most susceptible to fragmentation.
757 Others, including edge/gap species, insectivores that use mixed flocks facultatively,
758 hummingbirds and many frugivores, are far less vulnerable (Antongiovanni & Metzger, 2005;
759 Stouffer *et al.*, 2006, 2008, 2011).
760 In a similar vein, among bats, gleaning predators are consistently the most vulnerable
761 species whereas many frugivores respond positively to fragmentation and other types of forest
762 disturbance (Sampaio, 2000; Bobrowiec & Gribel, 2010; Farneda *et al.*, 2015; Rocha, 2016;
763 Rocha *et al.*, 2016). Many animal-eating bat species rarely persist in small (<100 ha)
764 fragments and in the secondary-forest matrix, reflecting trait-mediated environmental filters
765 that selectively benefit smaller fruit- and nectar-feeding species (Farneda *et al.*, 2015).
766 Primates exhibit similarly predictable patterns of species loss, with wide-ranging frugivores,
767 especially the black spider-monkey, being most vulnerable (Boyle & Smith, 2010a). Hence,
768 local extinctions in fragments follow a foreseeable pattern, with species assemblages in
769 smaller fragments rapidly forming a nested subset of those in larger fragments (Stouffer *et al.*,
770 2008). Random demographic and genetic processes may help to drive tiny populations into
771 oblivion, but the species that reach this precarious threshold are far from random.
772
773

774 **(2) Non-neutral extinctions**

775 An important corollary of nonrandom species loss is that fragmented forests are not neutral.
776 Neutral theory (Hubbell, 2001) assumes that species in diverse, space-limited communities,
777 such as tropical trees, are roughly equivalent in competitive and demographic terms. Making
778 these assumptions allows one to make predictions about phenomena such as species-area
779 curves, the relative abundances of species in communities, and the rate of species turnover in
780 space. Hubbell (2001) emphasizes the potential utility of neutral theory for predicting
781 community responses to habitat fragmentation: for isolated communities, locally abundant
782 species should be least extinction prone, with rare species being lost more frequently from
783 random demographic processes. Over time, fragments should become dominated by the
784 initially abundant species, with rare species gradually vanishing; other ecological traits of
785 species are considered unimportant.

786 Gilbert *et al.* (2006) tested the efficacy of neutral theory for predicting changes in tree
787 communities at the BDFFP. Neutral theory effectively predicted the rate of local extinctions
788 of species from plots in fragmented and intact forest, as a function of the local diversity and
789 mortality rate of trees. However, in most fragments, the observed rate of change in species
790 composition was 2-6 times faster than predicted by the theory. Moreover, the theory was
791 wildly erroneous in predicting which species are most prone to local extinction. Rather than
792 becoming increasingly dominated by initially common species, fragments in the BDFFP
793 landscape have experienced striking increases over time in disturbance-loving pioneer species
794 (Fig. 13) (Laurance *et al.*, 2006a), which were initially rare when the fragments were created.
795 As a model for predicting community responses to habitat fragmentation, neutral theory
796 clearly failed, demonstrating that ecological differences among species strongly influence
797 their responses to fragmentation.

798

(3) Key correlates of animal vulnerability

In the BDFFP landscape, the responses of animal species to fragmentation appear largely governed by two key sets of traits. The first is their spatial requirements for forest habitat. Among birds (Van Houtan *et al.*, 2007) and mammals (Timo, 2003), wide-ranging forest species are more vulnerable than are those with localized ranges and movements. Species with limited spatial needs, such as many small mammals (Malcolm, 1997), hummingbirds (Stouffer *et al.*, 2008), frogs (Tocher *et al.*, 1997) and ants (Carvalho & Vasconcelos, 1999), are generally less susceptible to fragmentation.

The second key trait for fauna is their tolerance of matrix habitats (Gascon *et al.*, 1999), which comprises regrowth forest and cattle pastures in the BDFFP landscape. Populations of species that entirely avoid the matrix will be demographically and genetically isolated in fragments, and therefore vulnerable to local extinction, whereas those that tolerate or exploit the matrix often persist (Laurance, 1991; Malcolm, 1997; Antongiovanni & Metzger, 2005; Ferraz *et al.*, 2007; Bobrowiec & Gribel, 2010).

At least among terrestrial vertebrates, matrix use is positively associated with tolerance of edge habitats (Laurance, 2004b; Farneda *et al.*, 2015), an ability to traverse small clearings (S. G. Laurance *et al.*, 2004; S. G. Laurance & Gomez, 2005), behavioral flexibility (Neckel-Oliveira & Gascon, 2006; Stouffer *et al.*, 2006; Van Houtan *et al.*, 2006; Boyle & Smith, 2010b) and a capacity to feed on early successional plants that thrive in the matrix (Farneda *et al.*, 2015; Rocha *et al.*, 2016; Meyer *et al.*, 2016). Within particular animal groups, such as beetles or small mammals, traits such as body size and natural abundance are generally poor or inconsistent predictors of vulnerability (Laurance, 1991; Didham *et al.*, 1998a; Jorge, 2008; Boyle & Smith, 2010a; but see Jorge *et al.*, 2015).

824 **(4) Key correlates of plant vulnerability**

825 Among plants, a different suite of factors is associated with vulnerability to fragmentation.
826 Because fragments suffer chronically elevated tree mortality, faster-growing pioneer trees and
827 lianas that favor treefall gaps are favored at the expense of slower-growing old-growth trees
828 (Laurance *et al.*, 2006a, 2006b). Pioneer species often flourish in the matrix and produce
829 abundant small fruits that can be carried into fragments by frugivorous birds and bats that
830 move between the matrix and nearby fragments (Sampaio, 2000; Nascimento *et al.*, 2006;
831 Rocha *et al.*, 2016). Especially vulnerable in fragments are the diverse assemblages of smaller
832 subcanopy trees that are physiologically specialized for growth and reproduction in dark,
833 humid, forest-interior conditions (Laurance *et al.*, 2006b). Tree species that have obligate
834 outbreeding systems, rely on animal seed dispersers or have relatively large, mammal-
835 dispersed seeds also appear vulnerable (Laurance *et al.*, 2006b; Cramer *et al.*, 2007b).
836 These combinations of traits suggest that plant communities in fragmented forests are
837 structured primarily by chronic disturbances and microclimatic stresses, and possibly also by
838 alterations in animal pollinator and seed-disperser communities. For long-lived plants such as
839 many mature-phase trees, demographic models suggest that factors that reduce adult survival
840 and growth—such as recurring wind disturbance and edge-related microclimatic stresses—
841 have a strong negative influence on population growth (Lindenmayer & Laurance, 2016).
842

843 **X. HORIZONS FOR NEW RESEARCH**

844 Although BDFFP researchers have attacked a diversity of research themes, some topics
845 remain poorly explored or enigmatic. For instance, there has been relatively little work to date
846 on the effects of fragmentation on the phylogenetic and functional composition of forests (but
847 see Didham *et al.*, 1998b; Andresen, 2003). A study that examined changes in the
848 phylogenetic structure of trees at the BDFFP concluded that most study sites—including

small and large fragments as well as intact-forest plots—exhibited a progressive decline over time in phylogenetic diversity (Fig. 14)(Santos *et al.*, 2014). This evidently occurred because tree genera that have increased in abundance across the study area are more closely related phylogenetically than are those that have declined. Do such changes reflect community-wide responses to large-scale drivers, such as global-change phenomena (Laurance *et al.*, 2004b), shifts in regional rainfall (S. G. Laurance *et al.*, 2009), or some other widespread event? Further study is needed.

Similarly, ecological interactions such as pollination and seed dispersal have been poorly studied at the BDFFP. Changes in pollinator assemblages (Dick, 2001; Dick *et al.*, 2003) might be expected to alter plant pollination, seed set, and gene flow among plants, but such effects are largely unknown. Could shifts in the abundance of old-growth tree species—such the decline of obligate outbreeders and species that require animal seed dispersers (Laurance *et al.*, 2006b)—reflect losses of key fauna in fragmented forests? Other ecological interactions, such as predator-prey, host-pathogen, and plant-mycorrhizal relationships, are virtually unstudied (but see Benitez-Malvido *et al.*, 1999).

Species invasions are also poorly understood in the BDFFP landscape. Taxon-specific studies suggest that the matrix supports a variety of plant, vertebrate, and invertebrate species that are foreign to Amazon rainforests, many of which are also detected in forest fragments (e.g. Brown and Hutchings, 1997; Tocher et al., 1997; Dick, 2001; Scariot, 2001; Laurance *et al.*, 2002, 2011). Do such invaders have significant ecological effects? Are they increasing in diversity or abundance over time, as might be expected as new invasive species colonize the study area? Are expanding roads and powerline clearings providing avenues for species invasions (Laurance *et al.*, 2009)? Are some species capable of invading intact forests? Are foreign pathogens arriving? An array of such questions remains unanswered.

Finally, there is considerable scope to use modeling approaches with BDFFP data to

generate long-term (≥100-year) projections about the fate of fragmented forests. One such study, using a novel neural-network approach, suggested that tree communities in forest fragments will become increasingly dominated by early successional species but that seed rain from forest interiors will continue to maintain a mix of pioneer and old-growth species, even near heavily disturbed forest edges (Ewers *et al.*, 2017). Another modeling study used data on elevated tree mortality and floristic changes from the BDFFP to make projections of long-term carbon-storage declines and shifts in plant-functional groups in fragmented forests (Groeneveld *et al.,* 2009).

XI. GENERAL LESSONS

The BDFFP provides a number of valuable lessons for environmental researchers and those working in developing nations. Here we highlight two conclusions of particular relevance.

(1) Values of long-term research

Many insights from the BDFFP would have been impossible in a shorter-term study. The exceptional vulnerability of large trees to fragmentation (Laurance *et al.*, 2000) only became apparent after two decades of fragment isolation. Likewise, the importance of ephemeral events such as El Niño droughts (Williamson *et al.*, 2000; Laurance *et al.*, 2001c) and major windstorms (Laurance *et al.*, 2007) would not have been captured in a less-enduring project. Many other key phenomena, such as the kinetics of species loss in fragments (Ferraz *et al.*, 2003), the strong effects of matrix dynamics on fragmented bird and bat assemblages (Antongiovanni & Metzger, 2005; Stouffer *et al.*, 2006, 2011; Meyer *et al.*, 2016; Rocha, 2016), the divergence of fragments in different landscapes (Laurance *et al.*, 2007) and the effects of fragmentation on rare or long-lived species (Benítez-Malvido & Martinez-Ramos, 2003b; Ferraz *et al.*, 2007) and alternative successional pathways (Mesquita *et al.*, 2015), are

899 only becoming understood after decades of effort.

900 Far more remains to be learned. For example, forest-simulation models parameterized
901 with BDFFP data suggest that even small (<10 ha) fragments will require a century or more to
902 stabilize in floristic composition and carbon storage (Groeneveld *et al.*, 2009), given the long-
903 lived nature of many tropical trees. Eventually, these fragments might experience a
904 fundamental reorganization of their plant communities, given major shifts in the composition
905 of their tree, palm, liana and herb seedlings (Scariot, 2001; Benítez-Malvido and Martinez-
906 Ramos, 2003a; Brum *et al.*, 2008) relative to those in intact forest. If these newly recruited
907 plants represent the future of the forest, then the BDFFP fragments could eventually
908 experience dramatic changes in floristic composition—comparable to those observed in some
909 other tropical forests that have long been fragmented (e.g. da Silva & Tabarelli, 2000; Girão
910 *et al.*, 2007; Santos *et al.*, 2010).

911

912 **(2) Training is vital**

913 Among the most enduring legacies of the BDFFP has been its leading role in training students
914 and environmental decision-makers. To date, the project has yielded over 700 technical
915 publications (http://pdbff.inpa.gov.br) and more than 200 Ph.D. and M.Sc. theses. It has also
916 trained more than 700 graduate students and conservation professionals in sponsored courses,
917 and hosted over 1,000 student interns to date. Many of those who have benefited from BDFFP
918 training are from Brazil or other Latin American nations. Among these are numerous
919 individuals who have now advanced professionally to hold important positions in government
920 agencies, universities and nongovernmental conservation organizations.

921 These training programs have had manifold benefits. For example, former BDFFP
922 students and researchers have led opposition to a Brazilian government scheme to settle
923 colonists in and around the BDFFP study area—an initiative that could bisect the Central

924 Amazonian Conservation Corridor, a complex of protected and indigenous lands that is one of
925 the most important conservation networks in Amazonia (Laurance & Luizão, 2007). BDFFP
926 trainees have also been leaders in documenting the impacts of major highways and
927 infrastructure projects that are crisscrossing the Amazon (e.g. Laurance et al., 2001a;
928 Fearnside & Graça, 2006) and that could promote large-scale human migration and forest
929 disruption (Barni *et al.*, 2015). A near-term threat to the BDFFP is a nearly completed
930 highway (BR-319) that will link the 'arc of deforestation' in southern Amazonia to Manaus
931 and the BDFFP, potentially promoting large-scale invasions or settlement of the study area
932 (Fearnside, 2015).
933
934 **XII. LESSONS FOR CONSERVATION**
935 We conclude by highlighting some important general lessons from the BDFFP for conserving
936 the Amazon and other tropical forests.
937
938 **(1) The BDFFP is a best-case scenario**
939 Although the BDFFP's forest fragments are experiencing a wide array of ecological
940 alterations, it is important to emphasize that it is a controlled experiment. The fragments are
941 square, not irregular, in shape. They are isolated by clearings of only 80-650 m width from
942 large tracts of surrounding mature forest. They are embedded within a relatively benign
943 matrix dominated by forest regrowth, not harsher anthropogenic habitats. In addition, these
944 fragments are largely free from ancillary threats, such as selective logging, wildfires and
945 overhunting, which plague many fragmented landscapes and wildlife populations elsewhere
946 in the tropics (e.g. Moura *et al.*, 2014). Such threats can interact additively or synergistically
947 with fragmentation, creating even greater perils for the rainforest biota (Laurance &
948 Cochrane, 2001; Michalski & Peres, 2005; Brook *et al.*, 2008). For these reasons, the effects

949 of fragmentation at the BDFFP are clearly modest, relative to many human-dominated
950 landscapes elsewhere in the tropics.
951
952 **(2) Reserves should be large and numerous**
953 A key conclusion from BDFFP research is that nature reserves in Amazonia should ideally be
954 very large—on the order of thousands to tens of thousands of square kilometers in area
955 (Laurance, 2005; Peres, 2005). Only at this size will they be likely to maintain natural
956 ecological processes and sustain viable populations of the many rare and patchily distributed
957 species in the region (Ferraz *et al.*, 2007; Radtke *et al.*, 2008). Such large reserves will also
958 provide greater resilience from rare calamities such as droughts (Feldpausch *et al.*, 2016) and
959 intense storms (Laurance *et al.*, 2007), facilitate persistence of terrestrial and aquatic animals
960 that migrate seasonally (Bührnheim & Fernandes, 2003) and buffer the reserve from external
961 threats such as fires, large-scale forest desiccation and human encroachment (Cochrane &
962 Laurance, 2002; Briant *et al.*, 2010).
963 Large reserves will also maximize forest carbon storage (Laurance *et al.*, 1997, 1998c)
964 and provide greater resilience to future climatic and atmospheric changes (Laurance, 2005,
965 2016; Peres, 2005). Further, on the ancient, nutrient-starved soils of central and eastern
966 Amazonia, low plant productivity translates into low population densities of many animals,
967 especially as one moves up the food chain, so reserves must be proportionately larger to
968 harbor viable populations of these species (Radtke *et al.*, 2008; Deichmann *et al.*, 2011,
969 2012). The recent observation that within-species genetic variation of terrestrial vertebrates is
970 higher in wilderness areas than in human-disturbed habitats further underscores the value of
971 large nature reserves for sustaining biological diversity and the capacity of species to adapt to
972 future environmental insults (Miraldo *et al.*, 2016).
973 Beyond large size, nature reserves in Amazonia should also be numerous and stratified

974 across major river basins and climatic and edaphic gradients in order to preserve
975 biophysically distinctive ecoregions (Olson *et al.*, 2001; Tscharnke *et al.,* 2012) and locally
976 endemic species (Bierregaard *et al.*, 2001; Laurance, 2007). In addition, the core areas of
977 nature reserves should ideally be free of roads, which facilitate human encroachment and
978 hunting, internally fragment wildlife populations and promote invasions of exotic species
979 (Laurance *et al.*, 2009).
980
981 **(3) No fragment is unimportant**
982 Tropical forests are being rapidly lost and fragmented (e.g. Myers et al., 2000; Sloan et al.,
983 2014), and a key question is whether smaller (e.g. <10 ha) forest fragments have much value
984 for nature conservation. We assert that there is no such thing as an 'unimportant' forest
985 fragment. In heavily fragmented landscapes, protecting remaining forest remnants is highly
986 desirable, as they are likely to be key sources of plant propagules and animal seed dispersers
987 and pollinators (Mesquita *et al.*, 2001; Chazdon *et al.*, 2008). They may also act as stepping
988 stones for animal movements in human-dominated lands (Laurance & Bierregaard, 1997;
989 Lima & Gascon, 1999; Dick *et al.*, 2003). In regions where forest loss is severe, forest
990 fragments could sustain the last surviving populations of locally endemic species,
991 underscoring their potential value for nature conservation (Arroyo-Rodríguez *et al.*, 2009).
992 Finally, the observation that regenerating forests recover floristic diversity far faster in
993 regions where small fragments of primary forest remain than in those lacking such fragments
994 underscores the vital role of retaining even tiny fragments of the original forest (Van Breugel
995 *et al.*, 2013).
996
997 **(4) Wounded landscapes can recover**
998 A further lesson is that fragmented landscapes, if protected from fires and other major

disturbances, can begin to recover in just a decade or two. Newly created forest edges tend to 'seal' themselves in a few years, reducing the intensity of deleterious edge effects (Camargo & Kapos, 1995; Didham & Lawton, 1999; Mesquita *et al.*, 1999). Secondary forests can develop quite rapidly in the surrounding matrix (Mesquita *et al.*, 2001), especially if soils and their seedbanks are not depleted by repeated burning and grazing (Ribeiro *et al.*, 2009; Norden *et al.*, 2011). Secondary forests facilitate movements of many animal species (Gascon *et al.*, 1999; Powell *et al.*, 2013), allowing them to recolonize fragments from which they had formerly disappeared (Becker *et al.*, 1991; Quintero & Roslin, 2005; Stouffer *et al.*, 2008; Bobrowiec & Gribel, 2010; Boyle & Smith, 2010a; Rocha, 2016; Rocha *et al.*, 2016). Species clinging to survival in fragments can also be rescued from local extinction via the genetic and demographic contributions of immigrants (Pimm & Jenkins, 2005; Zartman & Nascimento, 2006; Stouffer *et al.*, 2008). Compared to the BDFFP landscape, rates of forest recovery are probably slower in localities with severe forest loss, but such regions are likely to be of particular conservation significance and thereby worthy of efforts to reduce their recurring threats.

XIII. FRAGMENTATION AND LARGER-SCALE DRIVERS

(1) Interacting drivers

Taken in its entirety, it seems apparent from the large-scale, long-term research effort at the BDFFP that forest fragments and their biodiversity are being influenced by a variety of local and larger-scale factors. The intrinsic attributes of a fragment, such as its size, shape and degree of isolation from intact forest, are unquestionably important. However, these attributes are clearly modified by the features of the surrounding landscape and its dynamics over time. Such landscape features can influence the nature and magnitude of edge effects in fragments (Fig. 7), the permeability of the matrix for faunal movements, the composition of the seed

1024 rain entering fragments, the likelihood of destructive surface fires penetrating into fragments,
1025 and the intensity of abiotic forces such as microclimatic changes, wind turbulence and
1026 vegetation breezes (Fig. 3) that in turn can strongly influence fragment biodiversity and
1027 ecosystem processes.

1028 External vicissitudes, such as rare droughts, windstorms and intense rainfall events,
1029 can also leave a lasting imprint. Such phenomena might be influenced both by landscape-
1030 scale features as well as regional and possibly global climatic drivers. More generally, it is
1031 apparent that even intact forests in the BDFFP are experiencing concerted long-term changes
1032 in their composition and dynamics, which seem to reflect increasing forest productivity.
1033 These changes appear broadly consistent with those expected from increasing CO_2
1034 fertilization, although other environmental causes, such as declining cloudiness and increasing
1035 forest insolation, are also plausible. Whatever their causes, it is likely that the suite of changes
1036 observed in Amazonian forest fragments are partly a consequence of drivers operating at
1037 much larger spatial scales.

1038 In some cases, large-scale drivers could exacerbate ecological changes in forest
1039 fragments. For instance, elevated forest dynamics and proliferating lianas could result both
1040 from edge effects in fragments (microclimatic stresses and elevated wind turbulence that kill
1041 many trees) as well as from larger-scale drivers that increase forest productivity and
1042 dynamism while favoring fast-growing plant species (Laurance *et al.*, 2014b). In other cases,
1043 the larger-scale drivers might operate in opposition to local fragmentation effects. For
1044 example, the dramatic 'biomass collapse' observed in fragments from the mortality of many
1045 trees (Laurance *et al.*, 1997, 2000) might be partially countered by increasing forest
1046 productivity that in turn promotes faster tree growth—although this is likely to have only a
1047 modest effect given the pronounced loss of large, old-growth trees in fragments and their

replacement by smaller, lighter-wooded trees and vines (Fig. 6) that store much less carbon (Laurance *et al.*, 2006a, 2006b).

That fragments are being influenced by multiple drivers operating at widely varying spatial scales underscores serious complications for those seeking to understand and predict the effects of habitat fragmentation. Such drivers could interact in complex and potentially synergistic ways (Laurance & Useche, 2009), and it is virtually impossible to establish reliable experimental controls for global phenomena that may be operating everywhere (Laurance *et al.*, 2014b). Indeed, it is quite possible that even the most remote and seemingly pristine regions of the Earth are being influenced by certain global-change phenomena.

A further complicating matter is that even relatively modest differences between landscapes, such as rare weather events or subtle differences in land-use practices, could potentially multiply over time into far more pervasive changes. This idea is supported by the marked differences in trajectories of floristic change in forest fragments in the different cattle ranches (Fig. 11), even in a landscape as nearly uniform in its soils, climate, vegetation and land-use history as the BDFFP. This observation leads to the prediction that fragments within the same landscape will tend to converge in composition and dynamics over time, whereas those in different landscapes will tend to diverge. That such minor differences can seemingly provoke large consequences sends a strong note of caution for conservation biologists: it may be possible to make general predictions about the consequences of habitat fragmentation, but the interplay of local and larger-scale phenomena could render efforts to make precise local predictions or draw broad generalizations virtually impossible.

(2) The Amazon and climate change

Amazonian forests store roughly 150-200 billion tonnes of carbon in their live biomass (Malhi *et al*., 2006, Feldpausch *et al*. 2012), the release of which could seriously hinder

efforts to limit harmful climate change. Beyond this, Amazonian forests play vital roles in regional and global hydrological regimes, transporting massive quantities of moisture and heat to higher latitudes (Avissar & Worth, 2006; Nobre *et al.,* 2016). For such reasons, conserving tropical forests such as the Amazon is likely to have markedly greater benefits for limiting global warming than would protecting higher-latitude forests (Bala *et al.*, 2007).

Efforts to sustain the Amazon as a viable biophysical system can be guided by current research, which while constrained by uncertainties provides provisional guidelines for conserving the basin's forests (Nagy *et al.*, 2016). The best available information suggests that the destruction of more than 30-40% of all Amazonian forests could sharply increase the chances of a collapse of the crucial water-recycling functions that help to sustain Amazonian rainfall, especially during the critical dry-season months when forests are most susceptible to fire (Malhi *et al.*, 2008; Nobre *et al.*, 2016). With current Amazon deforestation levels at about 20% and large areas of additional forest being degraded by logging and surface fires and penetrated by new roads, hydroelectric dams, mining and other developments, there is clearly a real potential for further large-scale forest loss (Laurance *et al.*, 2001a; Fearnside, 2002, 2007, 2016a).

The ongoing fragmentation of the Amazon at a large spatial scale will clearly increase the chances of both planned and unplanned forest destruction, because fragmented forest tracts are far more vulnerable than intact forests to predatory logging, wildfires, climate change and other anthropogenic impacts (Cochrane & Laurance, 2002, 2008). Hence, a blueprint for conserving the Amazon and thereby reaping its bioclimatic benefits for humanity and the global ecosystem would be to greatly discourage further large-scale fragmentation while maintaining large, intact forest blocks that could potentially persist in perpetuity.

XIV. CONCLUSIONS

(1) In the heart of the Amazon, a large-scale, 38-year research project has revealed that the dynamics and community composition of fragmented rainforests cannot be understood simply as a consequence of local site attributes, such as fragment size or the surrounding topography. Rather, at least some ecological changes appear to result from interactions among local features and larger-scale changes occurring at landscape, regional and even global scales.

(2) In undisturbed forests, observed changes are consistent with those expected from rising forest productivity, and include accelerating forest dynamics, concerted shifts in tree-community composition, elevated growth rates for most tree species, and increasing abundances of disturbance-loving lianas. Plant fertilization from rising atmospheric CO_2 levels might explain these trends, although other causes are not implausible.

(3) In general, ecological changes in forest fragments are strongly influenced by edge and sample effects, the dynamics of the surrounding matrix of modified vegetation, and rare disturbances such as droughts and windstorms. Because of their high sensitivity to local vicissitudes, forest fragments in different landscapes are predicted to diverge over time in dynamics and community composition, whereas those in the same landscape may converge.

(4) Different species vary markedly in their vulnerability to forest fragmentation. Animal species that decline in abundance or disappear in forest fragments frequently have large area requirements and avoid the surrounding matrix, whereas susceptible plant species fare poorly in disturbed or edge-altered forests and often require vulnerable animal species for seed dispersal or pollination.

(5) Much of the Amazon overlays nutrient-starved soils where most plant and animal species are both rare and patchily distributed. This, combined with the increased vulnerability of fragmented forests to various human disturbances, suggests that Amazonian nature reserves

should be large (ideally $>10^4$ km^2) and numerous to ensure their long-term viability. Larger reserves will also be more resilient to future climatic change and extreme weather events.

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FIGURE CAPTIONS

Fig. 1. Map of the Biological Dynamics of Forest Fragments Project in central Amazonia.

Fig. 2. Habitat fragmentation in eastern Amazonia caused by a forest-colonization project (Tailândia) and cattle ranching (Paragominas). Forests are black and cleared areas are grey. Each scene shows an area of about 600 km^2 (adapted from Cochrane & Laurance, 2002).

Fig. 3. The vegetation-breeze phenomenon, which can promote forest desiccation in the general vicinity of pastures and clearings (from Cochrane & Laurance, 2008).

Fig. 4. Rates of tree growth in intact forests of the BDFFP accelerated over time for the large majority (84%) of tree genera (from Laurance *et al.*, 2004a). Data shown are mean rates of trunk-diameter growth for genera that increased or decreased significantly in abundance over time in the plots, as well as those that showed no significant trend. Interval 1 was 1984-1991, and interval 2 was 1992-1999.

Fig. 5. Increase in the abundance of lianas in intact-forest plots of the BDFFP (from Laurance *et al.*, 2014a). The solid line shows y=x whereas the dotted line is a linear regression fitted to the data.

Fig. 6. Negative association between liana abundance and the aboveground biomass of live trees in BDFFP forest-dynamics plots (from Laurance *et al.*, 2001b).

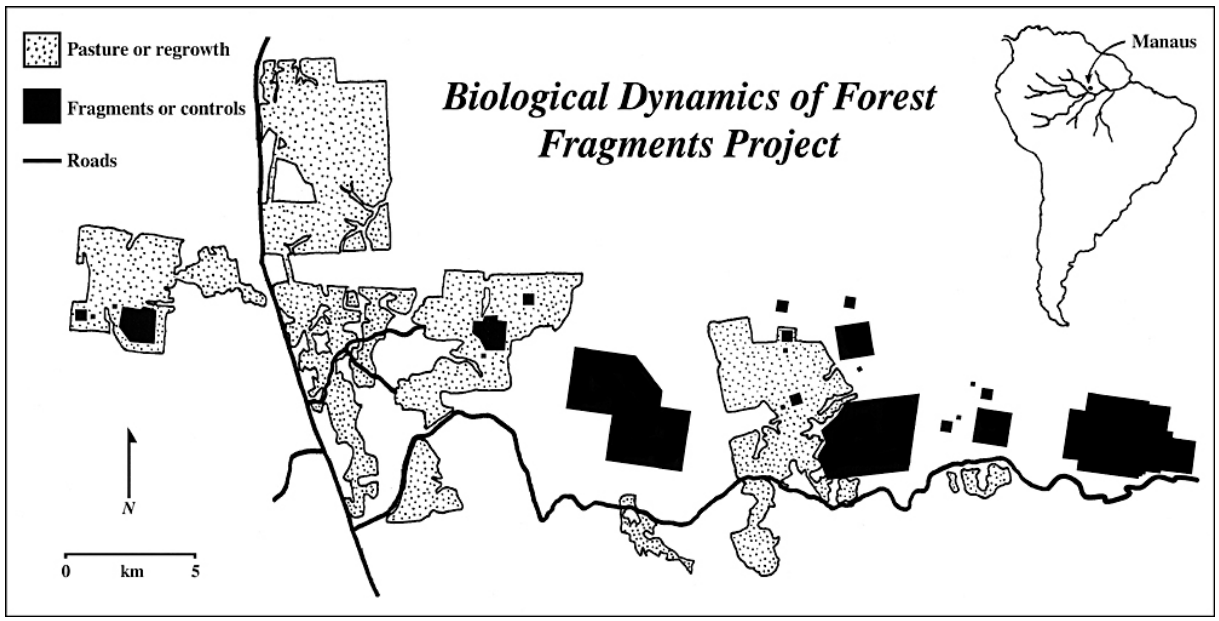
Fig. 7. The diversity of edge-effect phenomena studied at the BDFFP and the distance to

1936 which each was found to penetrate into fragment interiors (adapted from Laurance *et al.*,
1937 2002).
1938
1939 **Fig. 8.** The effects of single versus multiple nearby forest edges on (a) stand-level tree
1940 mortality and the (b) density and (c) species richness of disturbance-loving pioneer tree
1941 species. Values shown are the mean ± SD (from Laurance *et al.*, 2006a).
1942
1943 **Fig. 9.** Elevated temporal variation in butterfly species richness in fragmented forests. Shown
1944 is an index of variability in species richness for fragmented and intact sites sampled in
1945 consecutive years (adapted from Leidner *et al.*, 2010).
1946
1947 **Fig. 10.** Elevated temporal variation (coefficient of variation) in the number of tree stems per
1948 plot, shown as a function of distance from the nearest forest edge.
1949
1950 **Fig. 11.** Increasing divergence over time of tree-community composition in three fragmented
1951 landscapes at the BDFFP. Tree communities in forest-edge plots (<100 m from the nearest
1952 edge) are shown before forest fragmentation and 13-18 years after fragmentation, based on an
1953 ordination analysis. The ordination used importance values for all 267 tree genera found n the
1954 study plots (from Laurance *et al.*, 2007).
1955
1956 **Fig. 12.** Plots near forest edges (<100 m from edge) generally have higher tree mortality,
1957 more small trees, and more woody debris, relative to plots in forest interiors. Data shown are
1958 from an ordination analysis of 14 forest-biomass and necromass variables from 50 BDFFP
1959 plots (from Nascimento and Laurance, 2004).
1960

1961 **Fig. 13.** Striking increases over time in the density of 52 species of early successional trees in
1962 forest fragments in the BDFFP study area. Note that vertical axes are $\log_{10}$-transformed (after
1963 Laurance *et al.*, 2006a).
1964
1965 **Fig. 14.** Changes over time in the phylogenetic diversity of tree communities in 1-ha plots in
1966 the BDFFP study area (adapted from Santos *et al.*, 2014). Points with positive values (above
1967 the horizontal line) exhibited declining phylogenetic diversity over time, whereas those with
1968 negative values had opposite trends.
1969
1970

1971 Fig. 1

1972



1973
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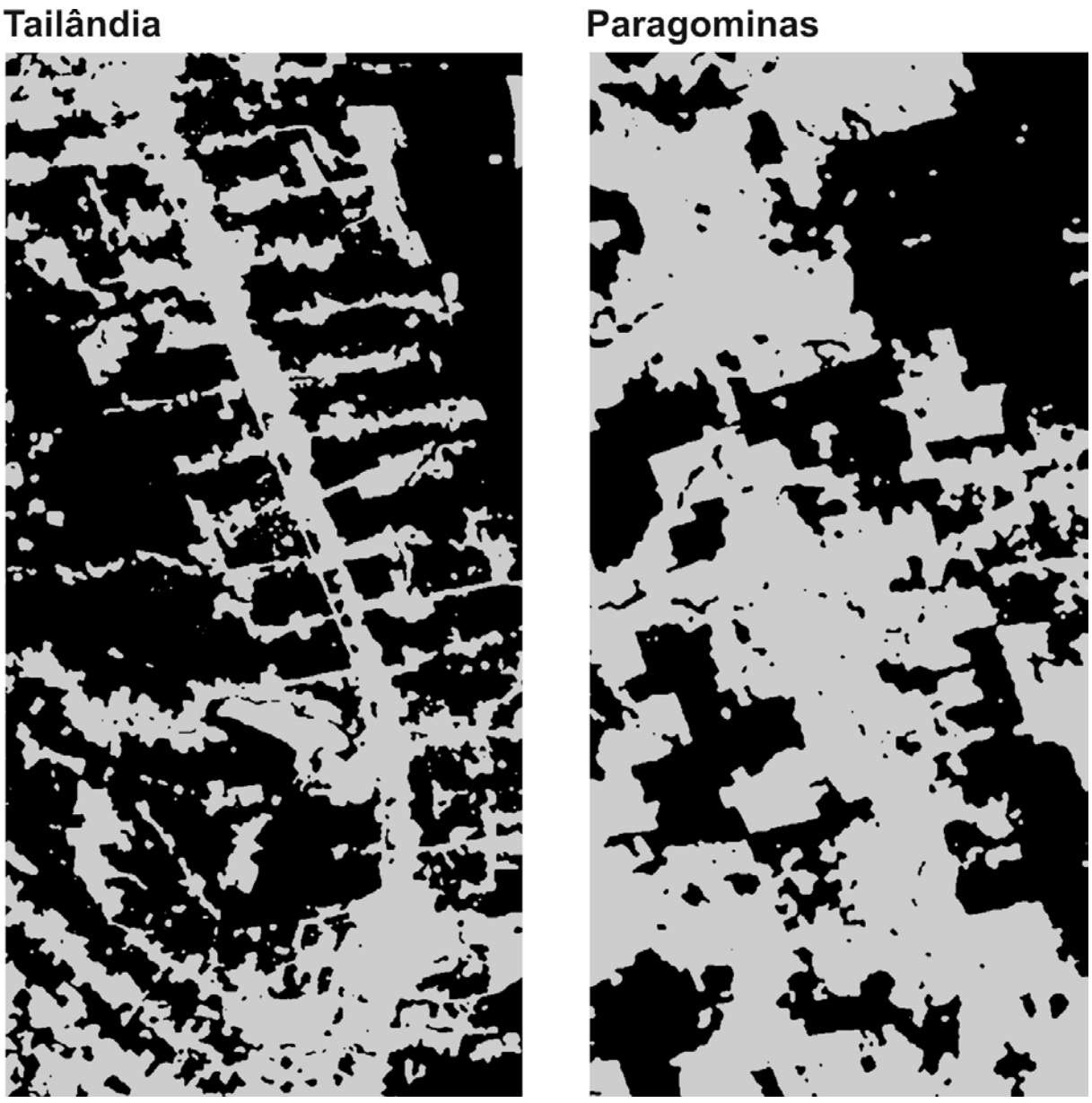
1975 Fig. 2

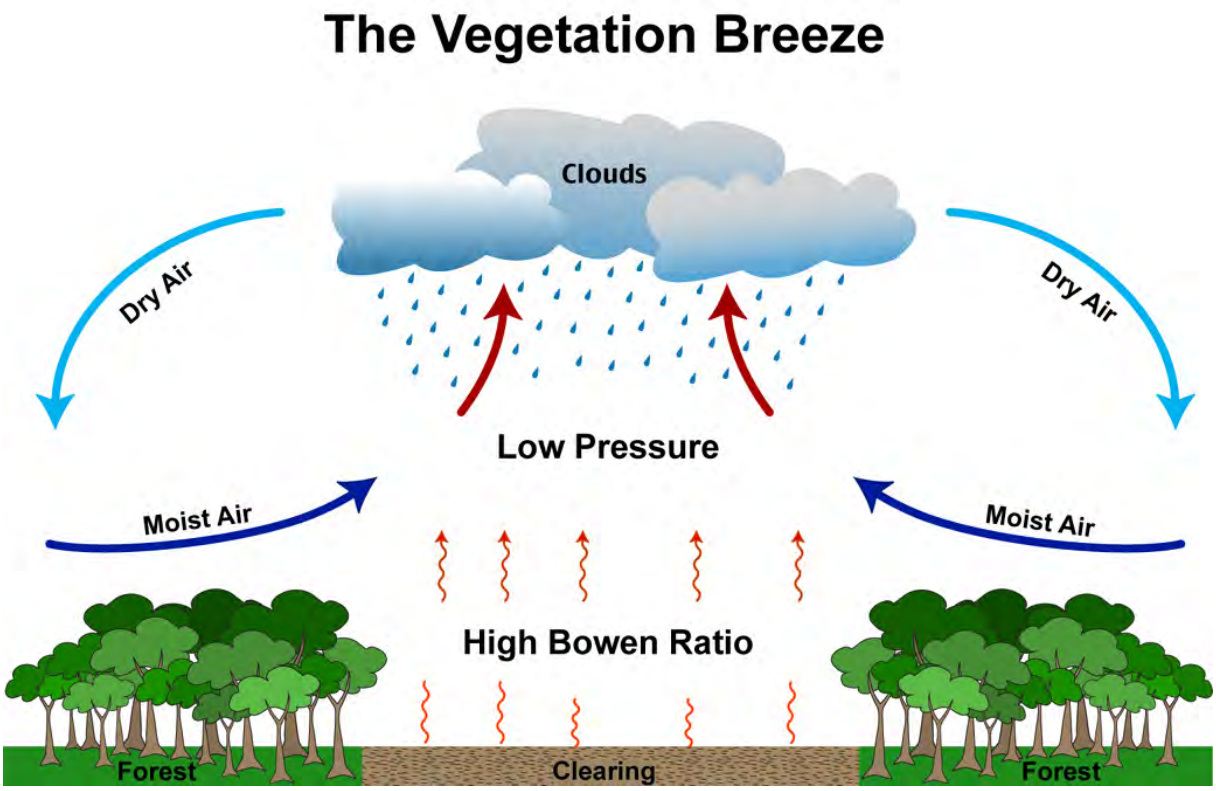
1976



1977
1978

1979 Fig. 3

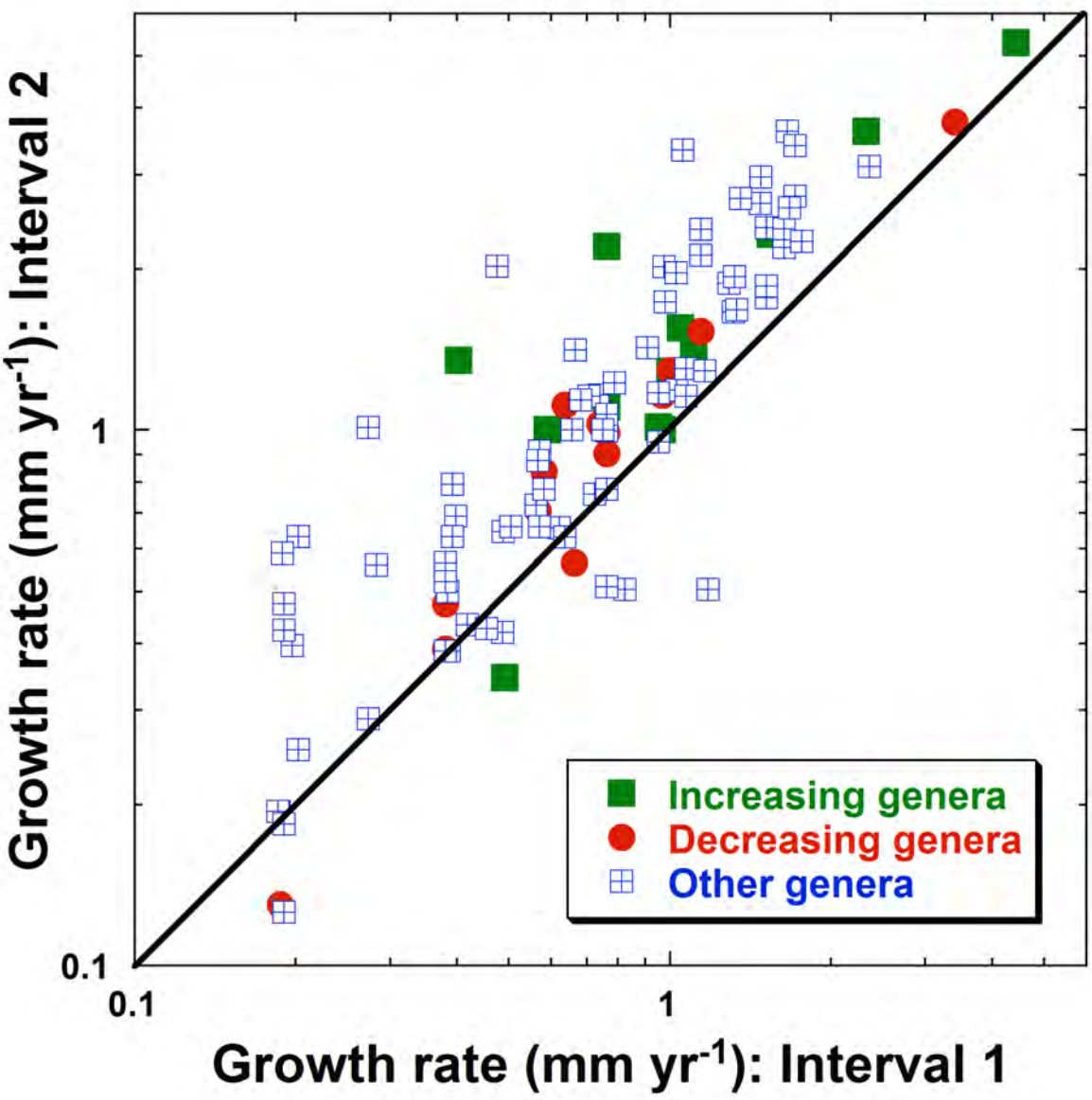
1980



1981
1982

1983 Fig. 4

1984



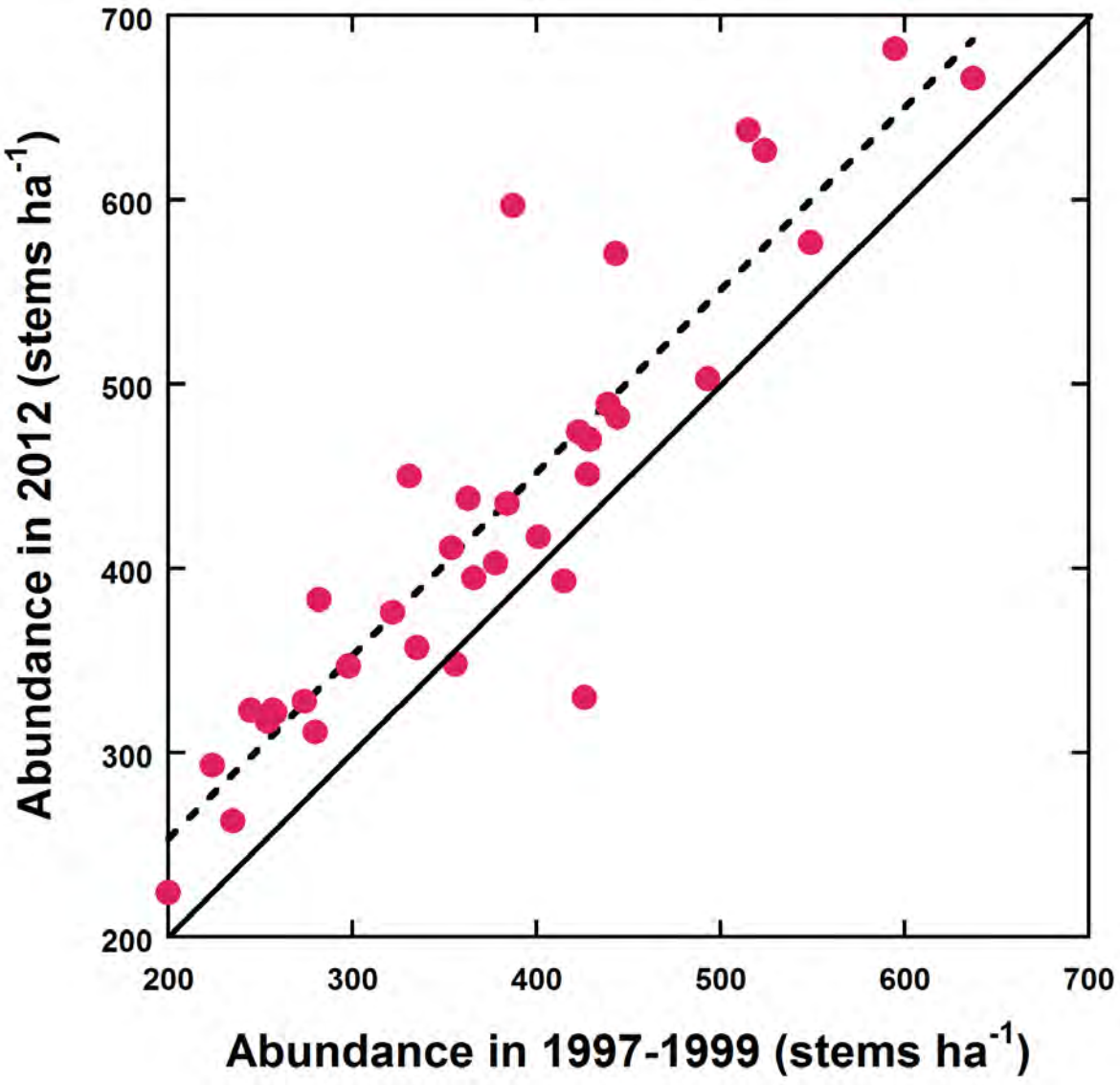
1985

1986

1987

1988 Fig. 5

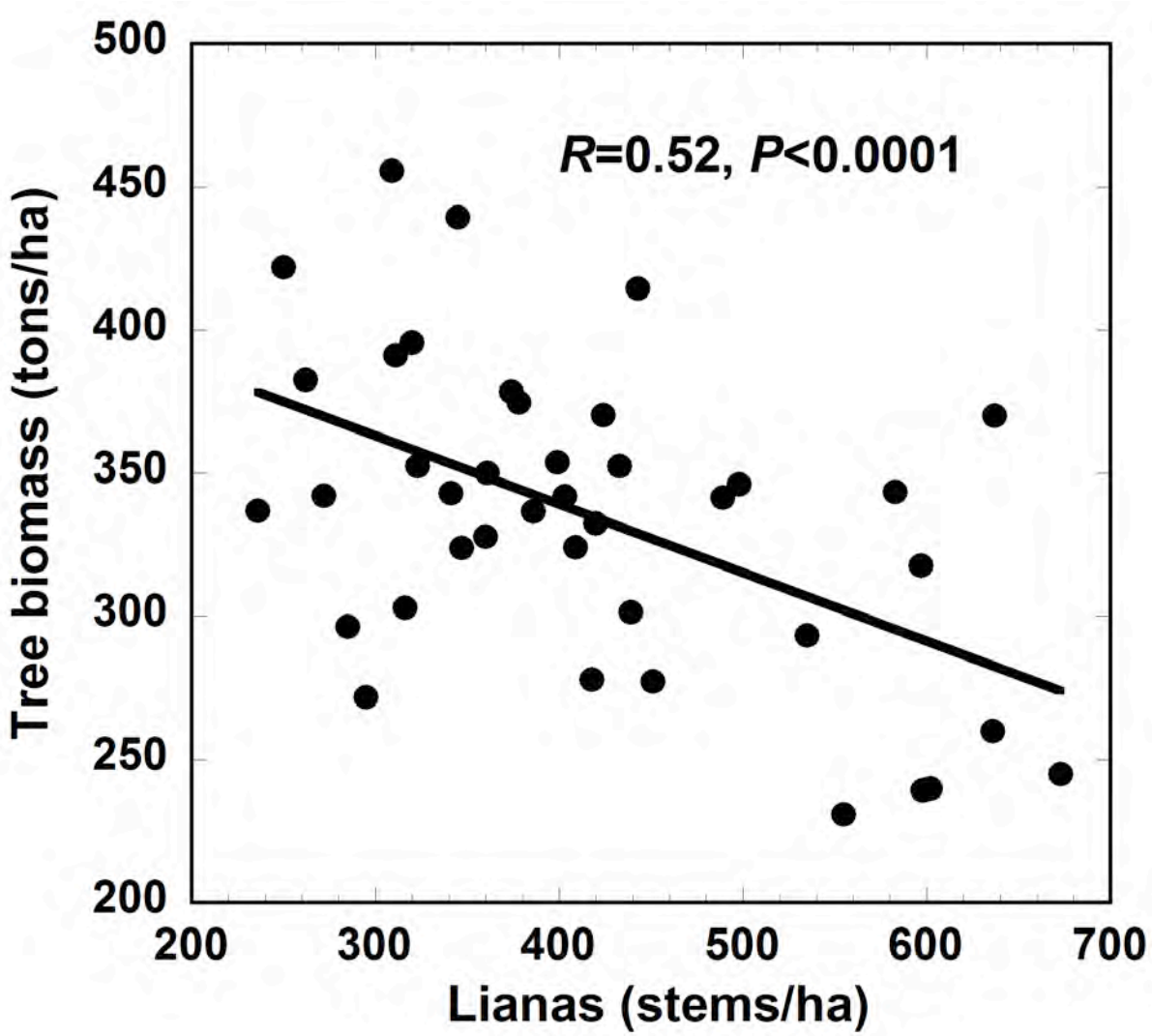
1989



1990
1991

1992 Fig. 6

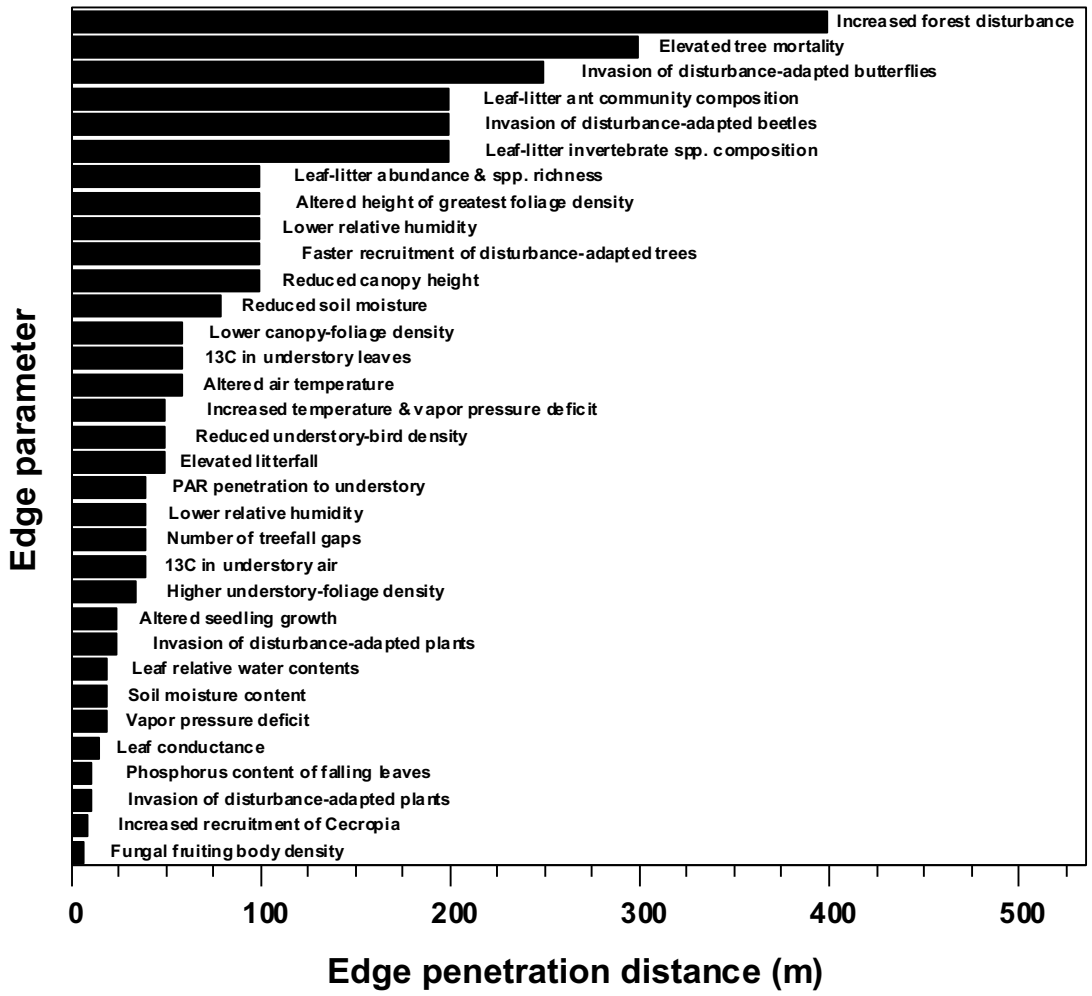
1993



1994
1995

1996 Fig. 7

1997



1998

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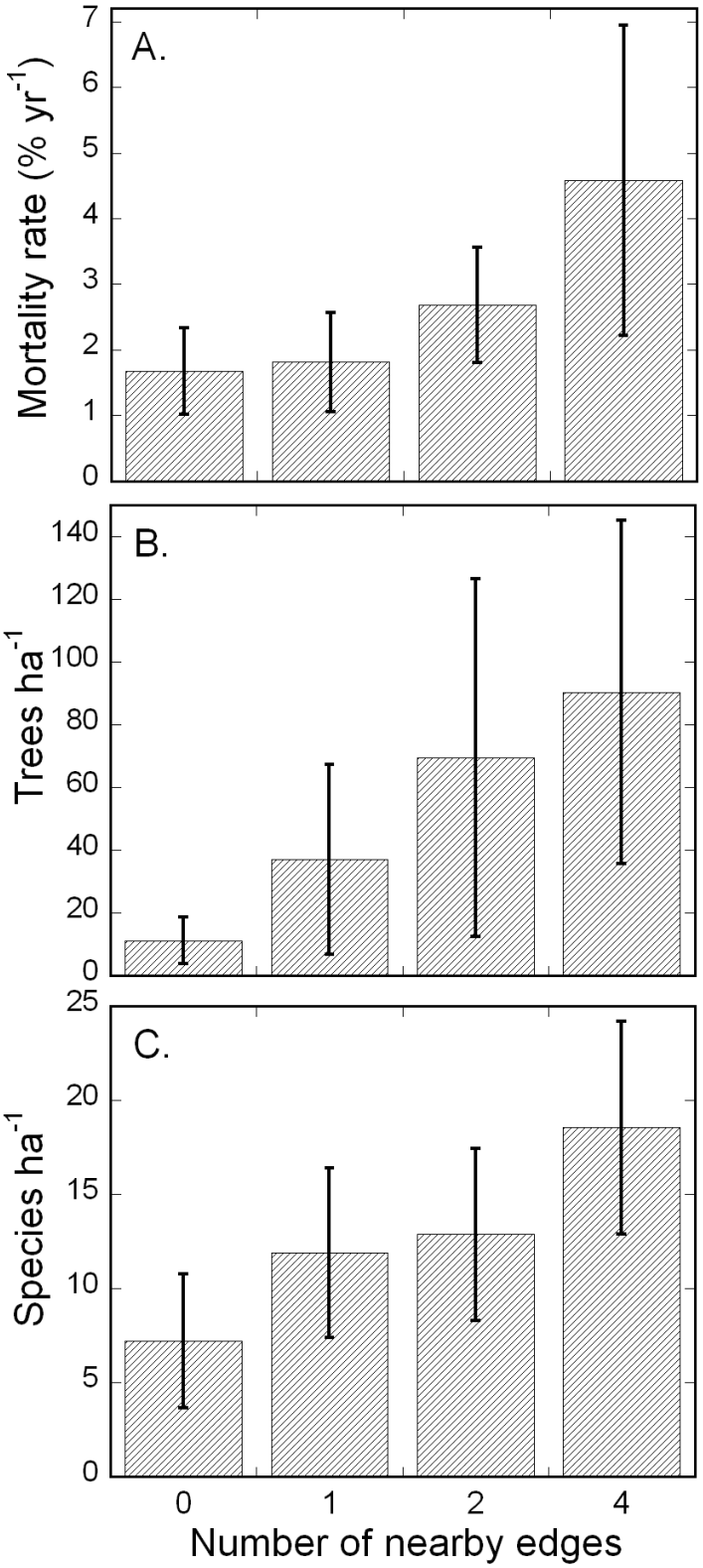
2001

2002 Fig. 8

2003

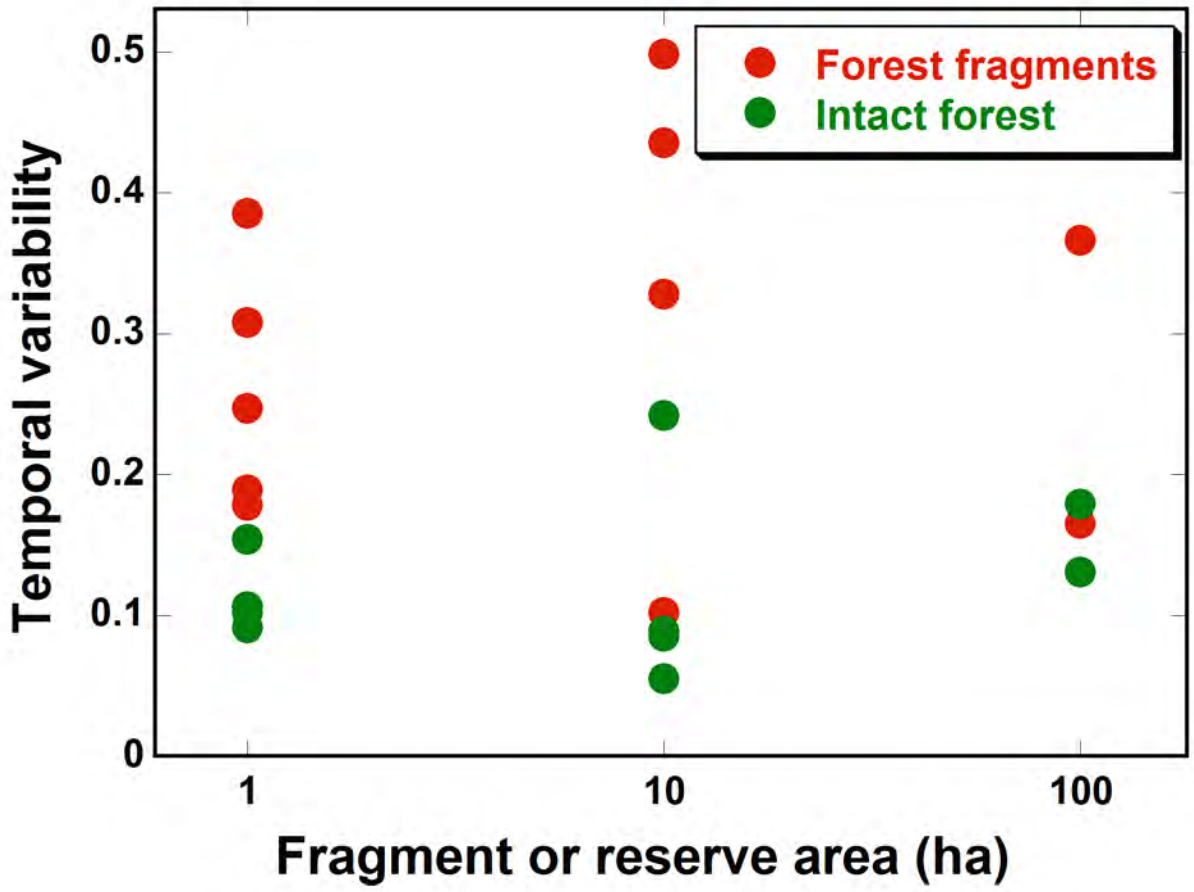


2004

2005

2006 Fig. 9

2007



2008

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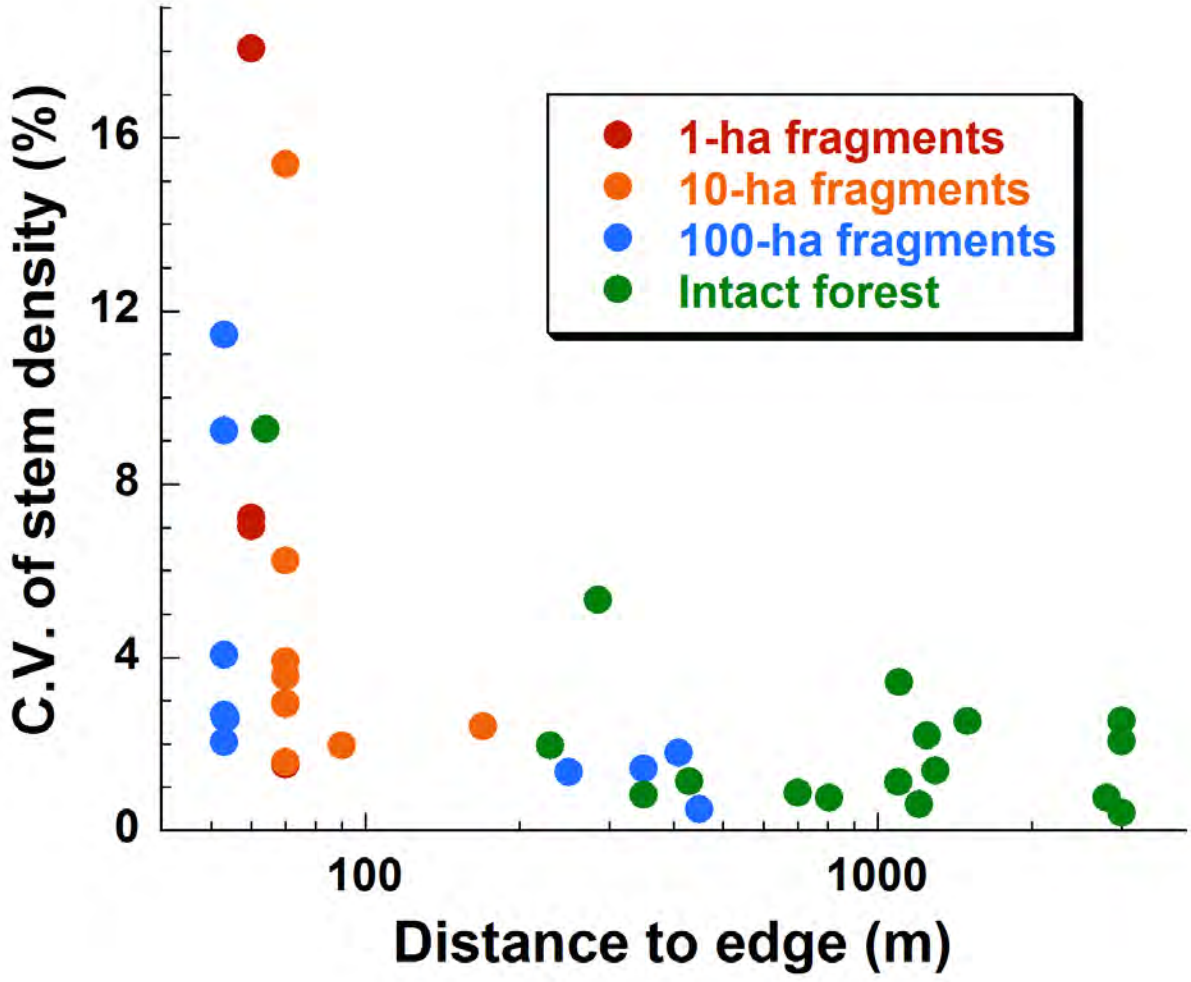
2010 Fig. 10

2011



2012

2013

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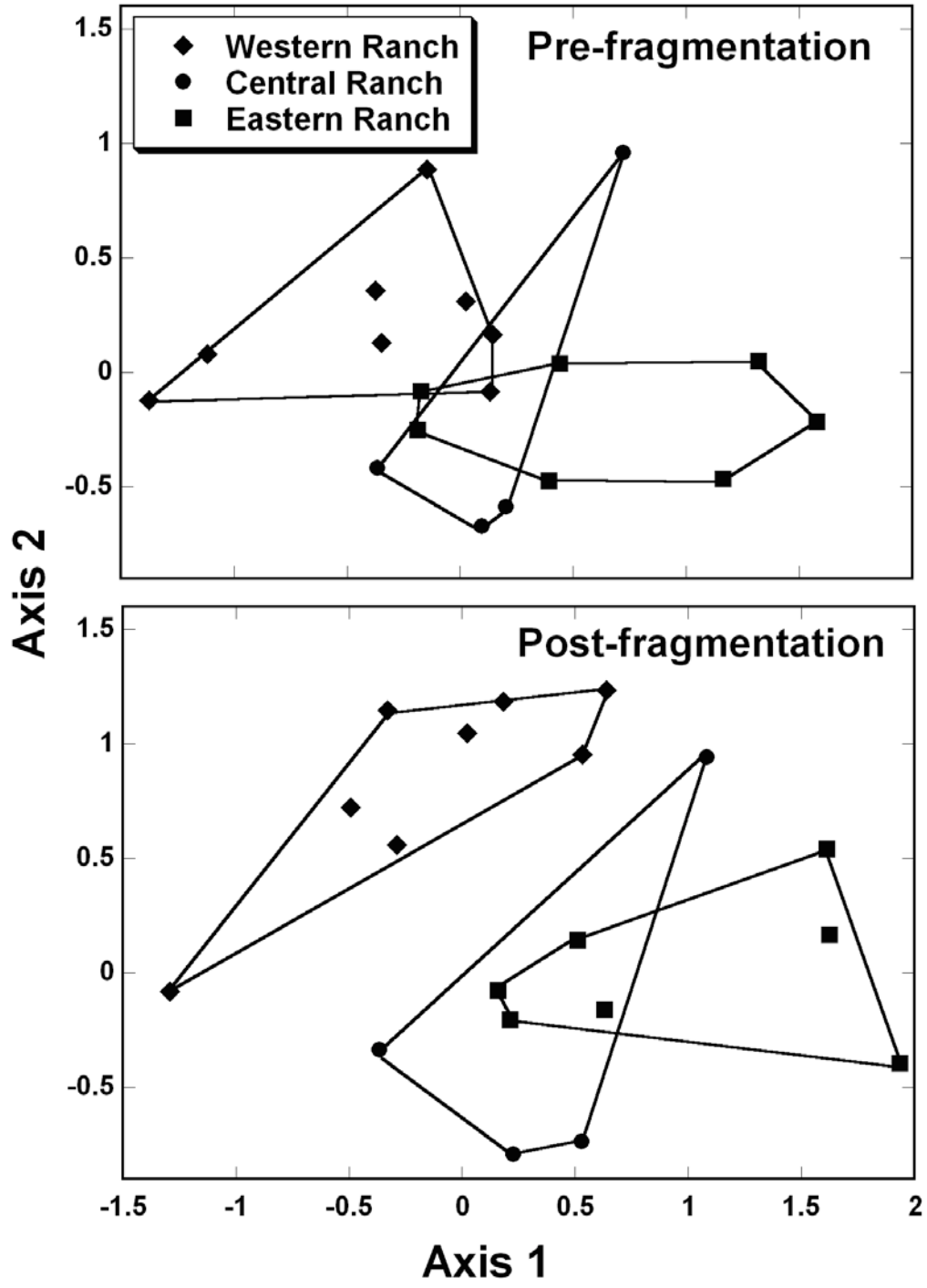
2015 Fig. 11



2016
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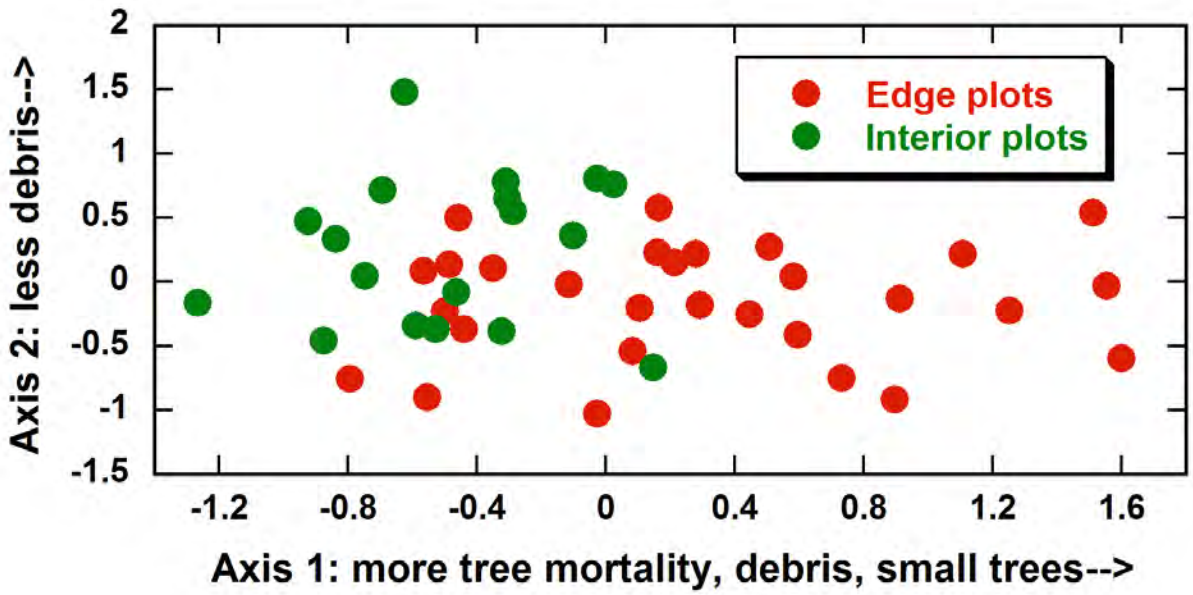
2018 Fig. 12

2019



2020

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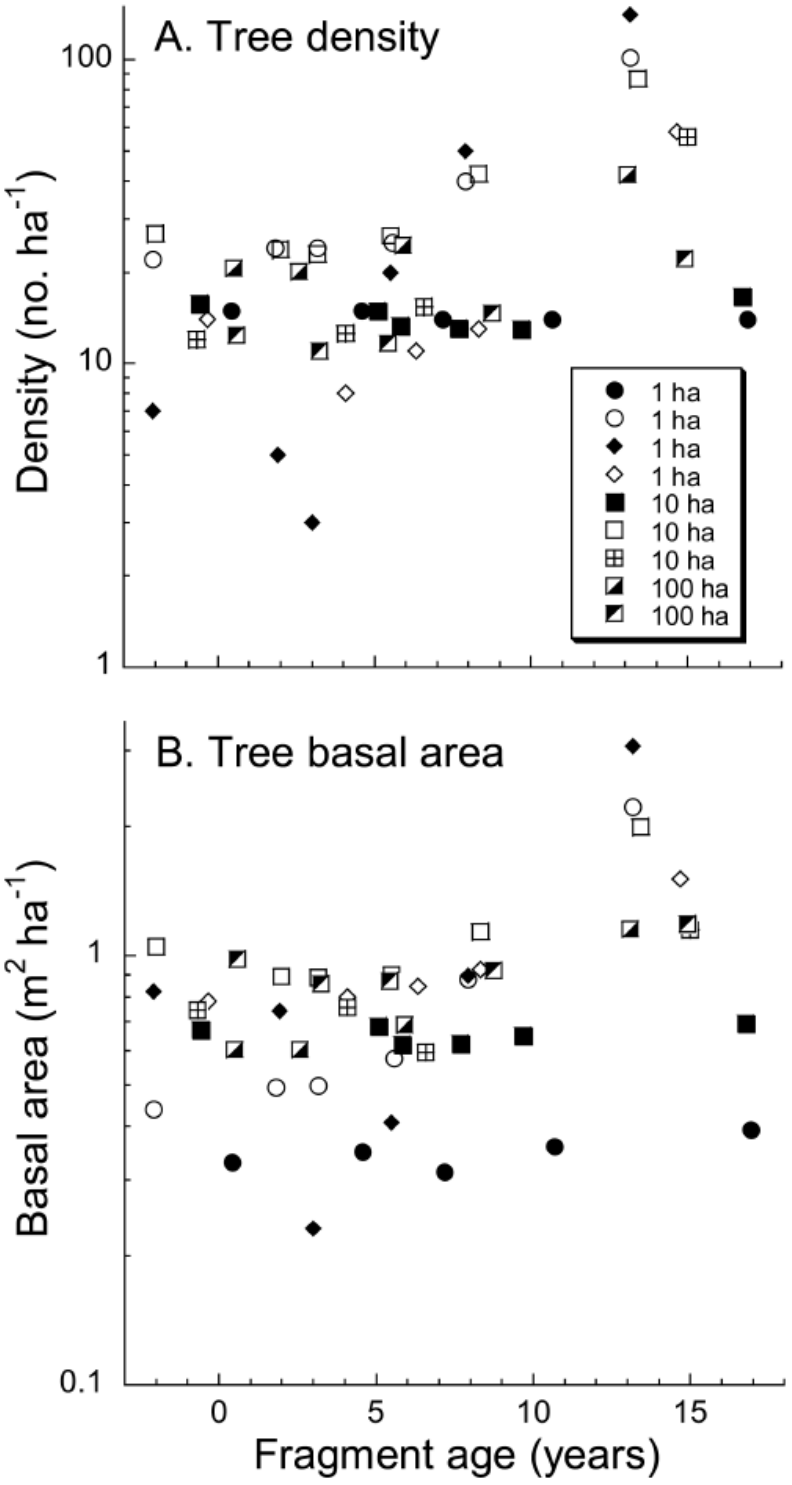
2025 Fig. 13



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2028 Fig. 14

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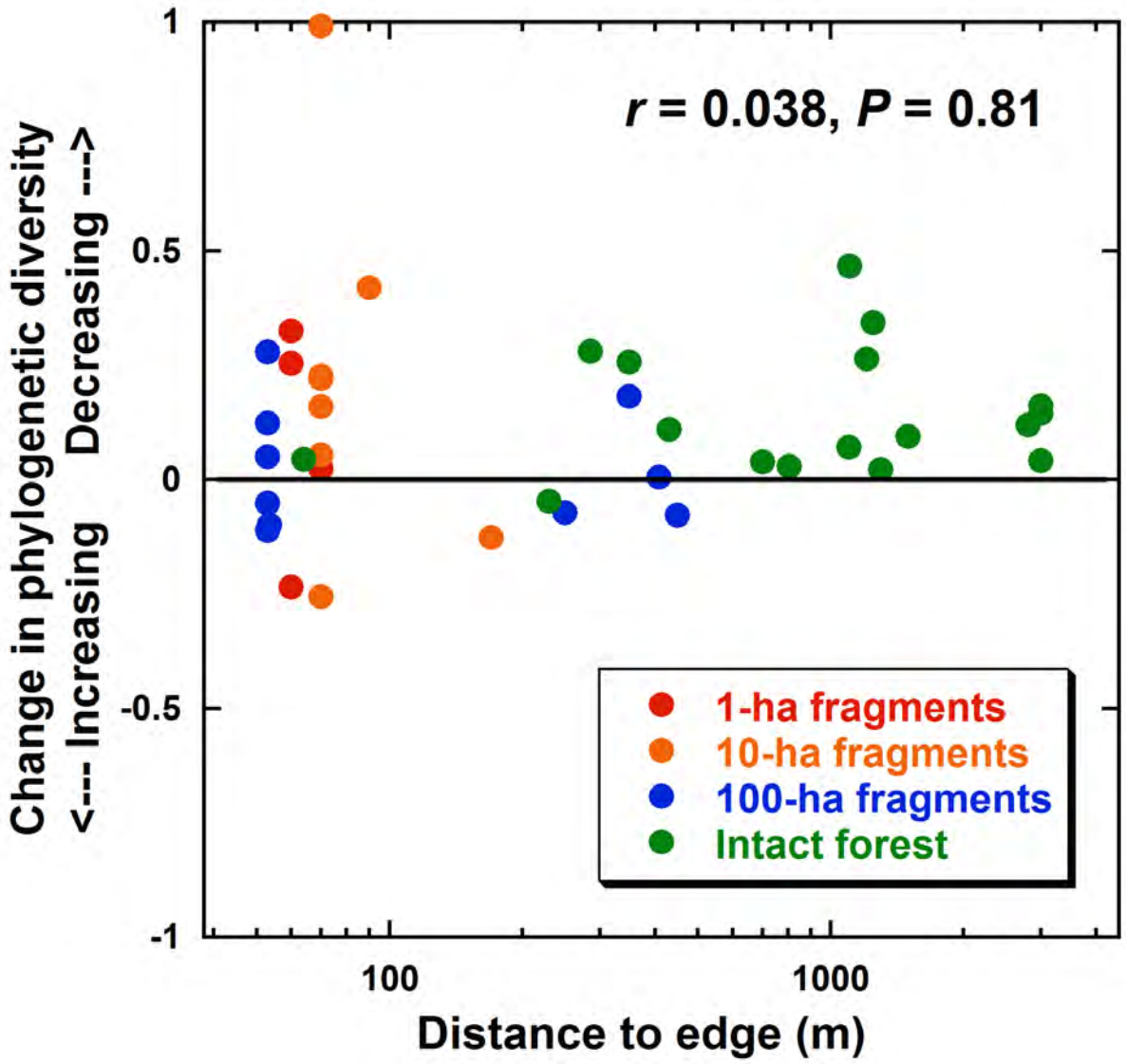

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